BOSTON UNIVERSITY

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Thesis

# THE RÔLE OF FLEAS IN THE TRANSMISSION OF *BACILLUS PESTIS*

by

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# CHAPTER I

# INTRODUCTION

## A. STATEMENT OF THE PROBLEM

The importance of determining the exact causative agent in the dissemination of _Bacillus pestis_ was recognized very early. The wide distribution of fleas and the readiness with which they attack new hosts are important facts in preventing the occurrence and spread of bubonic plague.

## B. WORK DONE ON THE PROBLEM BY OTHER INVESTIGATORS

Since the presentation of the rat-flea hypothesis by Simond (1898) much work has been done regarding the part played by fleas in the transmission of _Bacillus pestis_. Some of the earlier investigators were Galli-Valerio (1900), Nuttall (1902), Gauthier and Raybaud (1903), Noc (1905), and the Advisory Committee appointed by the Secretary of State for India, The Royal Society, and the Lister Institute to study plague in India (1906 to 1915).

## C. HISTORY OF THE PROBLEM

Because of the fact that early writers used the term plague to denite any pestilence in man or beast with a high mortality, it is almost impossible to determine which ones of these early diseases were bubonic plague.

Many reports list the first account of plague as having occurred in Lybia during the third century B.C. It was not until the sixth century, however, that plague spread to Europe and along the northern coast of Africa. In 1656 one of the most destructive of all epidemics occurred in Naples. It was during this century that the Great Plague of London destroyed a large proportion of the British population. Plague still prevailed extensively in Europe during the seventeenth and eighteenth centuries. Plague appeared in many localities during the nineteenth century. Epidemics were reported in Italy, Greece, and Egypt. Most cases of plague in the United States have been confined to California. However, one case each has been reported from the states of New York, Washington, and Louisiana.

D. DIFFERENT NAMES GIVEN TO PLAGUE

Pestis bubonica, levantine plague, oriental plague, black death, and malignant polyadenitis are a few of the synonyms for bubonic plague.

E. DIFFERENT THEORIES AS TO THE ORIGIN OF PLAGUE

For centuries the origin of the virus of infection of plague was suspected to be due to putrefaction of dead bodies brought about by improper disposal, or by great physical disturbances in the phenomena of nature. The disturbances themselves, or their effects, were also

suspected to be not only the originators of plague, but also the cause of pandemics and epidemics. Later it was believed that the plague virus was derived from the crude products of cadaveric decomposition polluting the soil and subsoil. Great calamities of a cosmic or telluric nature have been assigned as the cause, not only of the generation of the virus, but also of the virulence and diffusiveness necessary to render the disease endemic or pandemic. The discovery of the plague bacillus by Yersin and Kitasato working independently in 1894 disproved these hypotheses concerning the origin of plague.

## F. METHOD OF PROCEDURE

The discovery and characteristics of _Bacillus pestis_ are discussed. The major portion of the thesis is devoted to the discussion of the biology of fleas, the readiness with which fleas change and attack new hosts, the effects of the passage of _B. pestis_ through the alimentary canal of fleas, and of experiments performed by investigators to determine if the flea can transmit _B. pestis_.

# CHAPTER II

## DISCOVERY AND CHARACTERISTICS OF *BACILLUS PESTIS*

### A. DISCOVERY OF THE PLAGUE BACILLUS

*Bacillus pestis* was discovered and studied by Kitasato and Yersin, working independently at the same time (1894) during the epidemic of plague at Hongkong. Kitasato was part of a commission sent by the Imperial Japanese government to Hongkong to study the plague. Kitasato, in his bacteriological study of the plague, found numerous bacilli in the buboes (swellings of the inguinal glands), in the blood of the heart, in the lungs, liver, and spleen. Yersin was commissioned by the French Minister of Colonies to go to Hongkong to study the nature of plague, the conditions under which it spread, and to find more effective measures for preventing the spread of plague to French possessions. Yersin (1894) pointed out that the pulp of the buboes was filled in all cases with a short bacillus, thick-set, rounded at the ends, staining easily with aniline dyes, and not staining by Gram's method.

### B. CHARACTERISTICS OF *BACILLUS PESTIS*

1. *Bacillus pestis* is always found in the affected glands of well-marked cases of plague, in the buboes, in the blood and tissues of the septicemic variety, and in the lungs and sputum of pneumonic types of plague. In instances of a

well developed bubo it is possible to remove a few drops of fluid from the bubo by using a hypodermic needle. Cover-glass preparations and cultures may be made from the few drops thus extracted. The results of this method are often negative both culturally and microscopically for the hypodermic needle may fail to pierce the gland. In suppurating, discharging buboes it frequently happens that either the pus is perfectly sterile or it may contain only streptococci and other pyogenic organisms. In general the detection of _Bacillus pestis_ in the enlarged glands and in the blood of plague patients is more or less uncertain. No such difficulty, however, is experienced in cases of plague pneumonia. According to the observations of most investigators the blood-streaked sputum is usually rich in _B. pestis_. As regards the pneumonic type of plague, Childe (1898) states that the bacilli could be found in the profusion amongst the catarrhal epithelial cells and leucocytes which filled the alveoli, terminal bronchioles, and as well among the blood corpuscles of the alveoli into which the hemorrhage has occurred. Similarly, in the lungs of pneumonic (non) cases the bacilli could be seen, but in far less numbers, and mostly when hemorrhages had occurred in the alveoli. In dead bodies the bacilli are found in affected buboes and generally in the spleen, liver, lungs, bone marrow, bile, urine, peritoneal fluid, and fluid of the brain. It is this general distribution of the plague bacillus on corpses

which makes it imperative that special precautions be taken in the handling of dead bodies to prevent the spread of infection.

2. Simpson (1905) describes the typical plague bacillus as a short, thick, rod more or less ovoid in form. It measures from 0.5 to 0.75 micra in width and is usually from 1.5 to 2 micra in length. Klein (1906) observed from measurements made of different races of B. pestis that the longest bacilli occur in the bubo of the rat which has died of plague in nature and next in size are those of the bubo of man affected with plague, presumably through the rat. Simpson describes the bacillus as being more constant in breadth than in length, though it varies in breadth more than other bacilli. It varies considerably in shape and size, so that in microscopical examinations, in addition to the typical bacilli, very diverse forms may be seen. These forms include long and slender bacilli together with boat-shaped, dumb bell-shaped, and spherical microorganisms resembling cocci and diplococci in their appearance. This polymorphism may give rise to difficulty in recognition when plague appears in a locality for the first time and when the decision of the disease has to rest on a single case.

3. The bacillus is non-motile, the only motion being by Brownian movement. One or two terminal flagella have been observed and described, but they have been seen only

by a few.

4. The bacillus is easily stained by aqueous solutions of methylene blue, gentian violet, fuchsin, or any ordinary basic dyes, but is not stained by Gram's method unless a weakened spirit solution of 50% is used instead of absolute alcohol for the decoloration process. The bacillus is stained more deeply at the extremities than at the center and thereby acquires a very characteristic bipolar staining. The bipolar staining is more marked in bacteria taken from the tissues direct than from cultures, also in the ovoid, more than in the longer type of the bacillus. In some cases the unstained portion is not in the center but at the side or end of the bacillus, and in other cases the ends are not stained. The bipolar staining is well brought out by over-staining in carbol fuchsin for four or five minutes and then decolorizing with absolute alcohol, or by treating with acetic acid and then with carbol fuchsin. The bipolar staining is by no means constant in every bacillus, though in a plague specimen it is generally the predominant feature. In some smear preparations from infected tissues nearly all the bacilli show the bipolar staining; in others only a small portion exhibit this characteristic, and occasionally no bipolar staining is observed. Yersin (1894), Kitasato (1898), Cantlie (1899), Simpson (1905) and Rowland (1914) have observed the presence of a capsule under certain conditions. Klein (1906) denies the presence of any capsule. He believes

the reports of other investigators are based on the fact that in the staining process the ground substance, which is more or less stained, shrinks away from the bacilli, causing the latter to appear as if surrounded by a capsule.

5. The plague bacillus is distinctly aerobic growing easily on ordinary culture media as gelatin, broth, blood serum, and glycerine-agar; it also grows on milk and scantily on potatoes.

6. Haffkine (1897) showed that the bacilli grow in a very characteristic manner on bouillon. He states that this characteristic form of growth and the presence of involution forms are two important features by which the plague bacillus may be recognized.

7. In older pathological processes and in older artificial cultures as well as upon concentrated media, various degenerative forms are found. Galli-Valerio (1900) described several types of involution forms of Bacillus pestis. The first of these was the type found in cocoons. These forms are occasionally uniformly colored, sometimes only at the extremities where they appear from each side, as a sphere of protoplasm strongly colored. A second type is analogous to that of the preceding but bent about itself like a hook, presenting at one of its ends a ball of protoplasm strongly colored. Other forms encountered were elongated ones, rounded at both ends as if swollen; ovoid or rounded forms, analogous to those of the blastomycetes; those forms progressively swollen at the extremities, closely resembling

a club; pear-shaped forms--forms strongly swollen at one of the ends, while that of the other is short and thin; and filamentous forms. For the rapid production of involution forms Haffkine (1897) has recommended the use of agar-agar having a well marked alkaline reaction and a slightly dry surface. Vacuoles are sometimes observed in these involution forms. These involution forms may develop to such dimensions that they are twenty to thirty times the length of the ordinary bacillus. Some of these forms stain very well and uniformly, others show the bipolar staining, others take only a pale coloring throughout their substance, others stain only at the circumference, and others with vacuoles may not stain at all. These forms appear in old dry cultures of agar-agar and in cultures on potatoes. They do not appear in old or fresh bouillon cultures. Any change undergone in bouillon is that of disintegration.

8. Many experiments have been performed by several investigators in regard to the growth and virulence of Bacillus pestis when grown on various media; for example, squares of fabric, pine wood, paper, food products, merchandise, and clothing. In one experiment, Rosenau (1900) inoculated little squares of sterilized fabric (crash) with a three day old bouillon culture of Bacillus pestis. He found that the organism died after 13 days when kept at a temperature which occasionally rose to 27 degrees C. At a somewhat lower temperature the organism

remained alive and virulent for 48 days. Later, Rosenau (1901) tested the life history of Bacillus pestis on a variety of objects and under varying circumstances, the conditions of nature, however, being duplicated as nearly as possible. As a result of these experiments Rosenau pointed out that while food products may harbor the infective principle of plague, they are not to be feared much as far as their probability of carrying the infection is concerned. This does not apply to milk and its products, for milk is a good culture medium for B. pestis; and it was kept alive for 17 days in cheese and 72 days in butter. On the surface of food products B. pestis usually dies very quickly. It did not live for 24 hours on orange peel. Similar results were obtained by Rosenau with figs, raisins, and a large quantity of Chinese food products such as smoked and dried ducks, dried oysters, dried cuttle fish, dried ducks' gizzards, ducks' gizzards dried and placed in oil, smoked and dried pork, and duck eggs dried in a mixture of mud and rice chaff. All of these products were infected with B. pestis and kept at 37 degrees C. In rice B. pestis was found alive 13 days after inoculation. These facts indicate that B. pestis cannot live long on the surface of objects when dry at temperatures above 37 degrees C. B. pestis usually died in a few days when dried upon the surface of objects such as plush, carpet, paper, wood, sawdust, and bones. In porous substances, such as sponges,

it was found alive after 125 days when allowed to dry at 19 degrees C. At 37 degrees C., all other conditions being the same, it lived only two days. The bacillus was found to live for a long time in albuminous matter. Clothing and bedding were found especially subject to contamination from sputum and discharges from buboes and blisters. Articles so infected and kept in a cool, moist place retained the active infective principle a very long time. The work of Rosenau (1901) shows very plainly that clothing and bedding may harbor the bacillus for months. In seven tests made with cultures of the organism on paper, it was found that the organism usually died within 24 hours. At most it remained alive 8 days on paper allowed to dry, and 14 days on paper kept in a moist atmosphere. It may be concluded from the experiments of Kitasato (1894), Cantlie (1899), Rosenau (1901), Carougheau (1902), and Klein (1906) that the bacillus shows the quickest and most abundant growth on ordinary culture media when incubated at 37 degrees C.

9. Moisture is a very important factor in maintaining the life of the bacillus. The organism must have moisture in order to grow, and it may remain alive and virulent a very long time in the presence of moisture. On exposure to bright sunlight the bacillus usually dies. The report of Yersin (1897) that he had found organisms closely resembling <u>Bacillus pestis</u> in the earth of infected localities, and that these organisms could live in the soil

under unfavorable conditions led to much investigation as regards the saprophytic existence of B. pestis in the soil. The Indian Plague Commission (1901) states that the principle source of infection is to be found in houses in which the infection of plague has been introduced. Marsh (Indian Plague Commission, 1901) working with sterilized materials, was able to isolate organisms from moist sterilized garden earth 13 days after it had been contaminated, and from moist cow-dung for many months afterwards. Rosenau (1901) kept the plague bacillus alive for a long time in moist garden earth, especially when it was kept cool. He reports that the bacillus died very quickly in dry earth. He was able to keep the bacillus alive longer than 24 hours at any temperature in dry earth. The Advisory Committee (1906) published the results of their study concerning the saprophytic existence of B. pestis in the soil. This study had been made with cow-dung earth from the floor of a native house in India. The earth was grossly contaminated with virulent cultures of B. pestis and for several days afterward several attempts were made to recover the organism. The methods used were: (1) Cultures on plates made of Conradi-Drigalski medium and (2) inoculation into guinea pigs, four animals being inoculated subcutaneously each day with an emulsion of a weighed quantity of earth. The following results were obtained:

(a) 24 hours after contamination: out of seven attempts

the bacillus was recovered on every occasion by culture; the four animals all died of plague.

(b) 48 hours after contamination: out of seven attempts the bacillus was recovered once, while three out of the four guinea pigs died of plague.

(c) 72 hours after contamination: out of seven attempts the bacillus was recovered once, while three out of the four guinea pigs died of plague.

(d) 96 hours after contamination: again only once, out of seven attempts, was the organism recovered by culture, while only one animal out of the four died of plague.

The experiments were continued for 60 days, but on no further occasion was the plague bacillus isolated either by culture or by animal inoculation. These observations, then, would go to show that the plague bacillus in the cow-dung floors of native houses does not multiply but soon dies altogether; that, in short, it is incapable of leading a saprophytic existence in such a situation. It is further stated that floors of cow-dung grossly contaminated with B. pestis remained infective for 12 hours but not for 24 hours to susceptible animals which were allowed to run about freely on the floors; and that floors of chunam, (a floor made of a mixture of sand and lime, put down moist and allowed to set.), grossly contaminated with B. pestis remained infective for 6 but not for 12 hours, the infectiousness being tested by allowing susceptible animals to run about freely on them.

10. Different races of the plague bacillus have different powers of resistance to unfavorable influences. Some races are much hardier than others. Bacteria show quite a strong tendency to adaptability as do the higher animals. They may become accustomed to influences by a gradual survival of the fittest such that they finally resist conditions which would be fatal to the parent stock. <u>Bacillus pestis</u> often loses its virulence before it dies. In many of the experiments of Rosenau (1901) it was found that the time came when the organisms grew in bouillon, but lost its pathogenity for animals. This is an important fact from an epidemiologic standpoint, for an attentuated plague bacillus is probably harmless to man, even though its virulence can be increased by artificial means in the laboratory. These experiments plainly prove that either sulphur dioxide, when moist, or formaldehyde will kill <u>B</u>. <u>pestis</u> when applied in the strength and methods usually employed for these gases as disinfecting agents. In order to be effective there must be direct contact between the gas and the germ. In other words, these gaseous disinfectants can only be depended upon as surface disinfectants.

11. Wyman (1900) has pointed out that while <u>B</u>. <u>pestis</u> is so virulent, its resisting powers to chemical disinfectants is feeble, succumbing shortly in a 1 per cent. solution of carbolic acid or limewater. It dies in four days if kept at a dry heat of 60 degrees C. or in half an hour if subjected to a temperature of 100 degrees C.

12. <u>Bacillus</u> <u>pestis</u> is a well defined species as regards its morphological, cultural, and experimental characters. Under a number of circumstances, however, correct bacterioscopic diagnosis might be difficult. There are some bacteria which closely resemble <u>B</u>. <u>pestis</u> because of their pathogenic effect on some test animals as the guinea pig, or because of morphology, staining, and cultural characters. Most observers agree that <u>Bacillus</u> <u>pseudotuberculosis</u> <u>rodentium</u> Pfeiffer resembles <u>B</u>. <u>pestis</u> more closely than any other organism. The animal test on white rats is probably the best means for its differentiation. Klein (1906) has listed the following organisms as being mistaken for <u>B</u>. <u>pestis</u> under varying circumstances:

(1) <u>Proteus</u> <u>vulgaris</u> and its varieties or races.

(2) Pathogenic varieties of <u>B</u>. <u>coli</u> which by their characters belong to the group of <u>B</u>. <u>coli</u> and allies.

(3) <u>Bacterium</u> <u>Bristolense</u>

(4) <u>B</u>. <u>myoxides</u>

(5) <u>B</u>. <u>muris</u>

(6) <u>B</u>. <u>diptheroides</u> of mice

(7) <u>B</u>. <u>dansyz</u>

(8) <u>B</u>. <u>gaertner</u>

# CHAPTER III

# PLAGUE IN THE INDIVIUAL

## A. GENERAL CHARACTERISTICS OF PLAGUE IN THE INDIVIUAL

There are several symptoms which are characteristic of all types of plague of the severe type. These symptoms are the peculiar expression of the face, the halting speech, and the condition of the tongue.

## B. THE BUBONIC TYPE

The symptoms of bubonic plague are very characteristic and there should be little difficulty in making a diagnosis. Usually there is a fever, more often preceded by a few prodomata, associated with very painful glandular enlargements, severe headache, nausea, and vomiting. The fever is usually between 39.44 degrees and 40.55 degrees C., but may rise as high as 44.44 degrees C. or higher. There is a moderate leucocytosis associated with some media, and with a moderate diminution in the amount of hemoglobin. Buboes usually appear after the first onset of symptoms. The buboes form in the groin, neck, or axilla, or they may be confined to the abdomen. The size of the buboes varies according to the stage of development of the bubo and the character of the infection. Usually one gland of a group swells first, after which there is a rapid extension to the other glands of the group. The larger buboes are due to the swelling of several

glands and oedema of the adjacent tissues. In the fully developed buboes it is usually impossible to make out the indiviual glands which make up the swelling. The buboes are painful as a rule and are especially sensitive to pressure. In cases which prove fatal early the glands remain hard and painful, but in the majority of cases, owing to the matting together of the glands by a serous and sanguionelet infiltration, along with a mass of extravasated blood, the bubo enlarges and forms a doughy and bulky swelling. When the bubo is situated in the axilla or cervical region it is particularly dangerous when the exudation is extensive because the effusion is likely to become organized and converted into a hard mass, which may press on some vital part, or may form a slough. If the patient lives for seven or eight days the buboes either begin to resolve, or to show signs of softening accompanied by suppuration and sloughing. The skin may be very tense over the swelling. It usually looks thin and glossy. It is often reddened over the buboes, and occasionally vesicles or pustules appear on the surface. In very large buboes, especially in the cervical region, the jelly-like trembling which has been described can be easily made out. If the oedema becomes very extensive the buboes may be obscured. The pathologist distinguishes primary buboes of the first order, primary buboes of the second order, and secondary buboes. The first group includes the buboes appearing in the glands nearest the side of the inoculation, the second group

including the buboes formed by the extension of the bacilli directly through the lymphatics from the primary buboes to a second adjacent group of lymph glands. The third group includes buboes arising through the deposition of bacilli from the circulating blood in the lymph glands in any part of the body. Clinically it may be very difficult or impossible to distinguish primary buboes of the second order from secondary buboes. The clinically primary bubo is nearly always a primary bubo of the first order.

The remaining glands of the body in a bubonic case show either a normal appearance or a little engorgement of vessels. Lesions of engorgement or petechiae and extravasations have been described as occurring in the lung, liver, spleen, blood vessels, kidney, ureter, stomach, intestine, brain, and spinal cord. Sections of the skin in some instances show engorged capillaries with small hemorrhages where petechiae were visible on the surface.

## B. THE PNEUMONIC TYPE OF PLAGUE

In the early epidemics of plague the pneumonic type was often considered as a different disease from the bubonic plague because of the lack of the appearance of buboes. Many cases of plague in which there were no buboes are said by Batzaroff (1899) to have occurred in the epidemics which swept Europe and Asia under Marc-Aurele, 255-265 A.D., the Great Plague of Justinen in 542, and in the Black Death of

the fourteenth century.

Later many investigators demonstrated the presence of pneumonic plague. This form of plague is particularly dangerous because the clinical symptoms are not typical of ordinary plague, and it is more likely to be mistaken for bronchitis, broncho-pneumonia, or pneumonia. Pain, tenderness, and enlargement of the lymphatic glands in the inguinal, femoral, axillary, and cervical regions which are the most important external signs of bubonic plague are absent. Beyond coughing, fever, and a prostration which is exceptionally severe and far exceeding that which ought to be expected from the small amount of lung mischief discernible, there are few signs to raise suspicion that the disease is plague. The patient has a severe headache, nausea, vomiting spells, and pain in the limbs and body followed by a fever varying from 38.88 degrees to 40.55 degrees C. The respiration rate increases from 50 to 80 per minute, and signs of consolidation appear. The pulse is frequent and soon becomes feeble. An acute spleenic tumor can be made out. There may be sensitiveness in the region of the various lymph glands of the body. More or less pronounced coughing with dyspnoea sets in, and a quantity of watery sputum tinged with blood, and becoming profuse as the disease advances, is coughed up as a rule without effort. The sputum is not the glairy, viscid rusty character of acute pneumonia, though on the clothes it may be readily mistaken for this. Most sounds are heard at

the base of the lungs and over the pneumonic patches; but however hurried the breathing and quick the rate of pulse, there is not that disproportion between the pulse and respiration ratio which occurs in acute pneumonia. The symptoms become rapidly worse, the patient becomes delirious, the heart action, with or without coma gradually fails and death occurs on the fourth or fifth day, or earlier. The description of the remaining internal organs already given applies equally to this form of plague, except that the large hemorrhages are absent, but the petechiae on the surface of the heart, in the pelvis of the kidney, in the bladder, in the stomach, and in the intestines are commonly present. Petechiae in the skin are not observed in this form of plague.

## C. THE SEPTICEMIC TYPE

One can think of _Bacillus_ _pestis_ getting in the blood in cases of primary plague septicemia (sometimes called the toxic and siderous type) in various ways. When a human being or animal is extremely susceptible it is conceivable that the bacillus could enter through the skin and pass through the lymph glands, and so into the blood without setting up primary buboes. In the same way it could enter through the conjunctiva or other exposed mucous membranes. In septicemic plague the fever is high, the pulse is frequent and feeble, and delirium and coma may occur. A spleenic tumor rapidly develops and is often associated with

acute pains in the left side. There is tenderness over all the lymph glands of the body. Frequently there are hemorrhages in the skin or in the mucous membranes of the lungs, stomach, intestines or urinary passages. In some cases the bacilli can be frequently found in cover-slip preparations made from the blood. Cultures from the blood are, however, more reliable for the discovery of the bacilli, and animals inoculated with a few cubic centimeters of blood die with typical lesions of plague. Death may occur in from one to three days from the time the patient is first attacked or even after the lapse of a few hours.

Secondary plague septicemia exists when in cases of bubonic plague some of the bacilli get into the blood. It is these bacilli which account for the secondary buboes. In many of the fatal cases of bubonic plague the bacteria go over into the blood and multiply in great numbers, so that the blood and spleen at death and shortly before, contain large numbers of bacilli. In cases of the bubonic form of the disease, it may be that such a general bacteraemia does not occur, the process remaining essentially localized to the primary buboes, or, if a few bacilli get over into the blood, they are filtered out by the organs, and give rise to either secondary buboes or to noticeable phenomena.

## D. MILD PLAGUE OR PESTIS AMBULANS

At the beginning and end of large epidemics it is

common to find numbers of cases of plague which are so mild that they cause the patients but little inconvenience, and many of these may pass unrecognized. This type of plague, mild plague or pestis ambulans is likely to escape attention more readily than the pneumonic type because of the slight constitutional disturbance which it may produce, and because it is often taken for some other disease. The great importance of these mild cases of plague for the spreading of the disease is evident. Since the bacilli are given off through the urine and feces, a mild cases of plague may spread the bacilli far and wide.

## E. CUTANEOUS PLAGUE

The existence of cutaneous plague has been denied by some investigators. It seems clear, however, that primary infection of the skin with the plague bacillus is a recognized form of the disease. The cutaneous lesions take the form of vesicles, pustules, or carbuncles. Primary infections of the skin are certainly very unusual. The absence of primary infections of the skin, and the absence of lymphangitis between the point of entrance of the bacilli and the first lymph glands to be infected are the characteristic features in the majority of cases of the disease.

## F. TONSILLAR PLAGUE

The buccal mucous membranes form one of the portals of entry of the plague bacillus into the body. It is probable

that the cervical buboes arise from that source of infection. Of all the buccal structures, the tonsils seem to be the most frequently attacked. The tonsils suffer changes unlike those described in the primary lymphatic buboes of the first order. There is congestion, hemorrhage, necrosis of cells, and extensive growth of bacilli. The bacilli are spread beneath the layer of stratified epithelium, elevating this layer through their excessive growth. The epithelium shows vacuolation and loss of nuclei. Occasionally masses of bacilli occur in the deeper layers and even within the lumen of the glands. The appearance here presented is not unlike that described of the primary plague pustules. The adjacent glands suffer along with the tonsils; their enlargement constitutes, of course, the cervical buboes.

## G. SYLVATIC PLAGUE

The Sylvatic Plague Committee (1937) reports the occurrence of five cases of sylvatic plague in California. The usual symptoms were fever from 38.88 to 41.11 degrees C., pulse around 96, respiration 22, and general swelling in the axillarly region. Despite the serious septicemic nature of the infections, the patients made uneventful recoveries. The strains involved pass the same infectiousness for guinea pigs as established for other cultures isolated from man and rodents during 1933-1935.

## H. ADDITIONAL TYPES AS DESCRIBED BY CANTLIE

In addition to the types already described, Cantlie (1899) lists the following other types:

(1) The intestinal type in which occurs an intestinal flux, consisting at the onset of diarrhea, to be followed later by the appearance of blood mucus, and epithelium in the stools.

(2) A cerebral type referring to that form in which the nervous symptoms are so pronounced as to put all other minor evidences of the disease in the background. Delirium, muscular twitchings, loss of consciousness, and deafness often occur.

(3) Puerperal cases in which hemorrhage from the uterus and miscarriage are the prominent features of an attack.

(4) A typhus type implies a resemblance between plague and malignant typhus fever. Though plague has been termed the typhus of the tropics, there is no etiological affinity between the two diseases, but not infrequently the symptoms of the two are almost alike, even to the skin eruption.

# CHAPTER IV

# PLAGUE IN ANIMALS

## A. Class Mammalia

### 1. Order Primates

It is said by Clemow (1900) that on three separate occasions monkeys have been observed to sicken and die from a disease resembling plague at the time of an epidemic of plague in man. On each occasion the specific nature of the disease in these animals was proved bacteriologically. Under artificial conditions the common brown monkey (Macacus radiatus) and the common gray monkey (Semnopithecus entellus) are very susceptible to the action of the plague bacillus when pure cultures are artificially introduced into their tissues.

### 2. Order Marsupalia

#### a. Family Didelphyidae

Bandicoots (Nesokia bandicota), which is common enough in India, though much less common than the ordinary house rat, has been known to become infected with plague.

### 3. Order Rodentia

#### a. Family Leporidae

Rabbits, though susceptible to the disease in the laboratory, do not appear to have contracted the disease under natural conditions. Experiments with the rabbit in regards to its susceptibility to plague, led DeSouza, Arruda,

and Pinto (1910) to conclude that this animal, on Terceira Island, is very susceptible to plague.

b. Family Muridae

(1) When rats are attacked with plague they usually leave their underground habitations and migrate, often for a considerable distance. Thompson (1906) includes four species of rat under the term "rats". These are Mus decumanus, the gray rat; Mus rattus, the black rat, with its variety Mus alexandrinus rufus; and Mus musculus, the gray mouse. All of these suffer from plague in nature. Plague in the rat may be characterized by one or more well defined buboes, or not any buboes, but a general enlargement of the lymph glands. Some buboes are more or less softened or caseous upon sectioning while others are distinctly hemorrhagic. The buboes are as a rule located in the groin, axilla, or pelvis. The disease appears usually to become septicemic before the death of the rat, and the bacilli can be found in many parts of the body. Severe affection of the nervous system is also evidently present, just as in man, as is indicated by a staggering gait, spasmodic and paralytic symptoms, and by a dazed appearance. Rats living in burrows in the soil might become infected by the constant grubbing with their noses in the dust and surface layers of the soil. It is regarded as probable that rats may become infected with plague from grain or other food that has been infected by the ejecta or sputa of other animals dead of plague. Clemow (1900) states that a

plague epizootic in rats may start and also be perpetuated by their eating the dead bodies of the infected animals--including human beings and also other rats.

(2) Plague has been produced in rats artificially in a variety of ways. The common methods are: inoculation with pure cultures of the bacillus, by implantation of fragments of organs from plague cadavers under the skin of rats, by feeding with the infected material, by intraperitoneal injection of plague material, and by placing fragments of organs or a portion of a pure culture of the bacillus in the nostrils or conjunctiva.

(3) A considerable immunity to plague infection is said by McCoy (1906b) to exist among the wild rats of San Francisco. The percentage of immunity is especially high among the old rats. The immunity encountered was probably natural in most cases.

(4) _Mus decumanus_ lives in burrows, basements, rights-of-way and sewers. This species has also been found far away from any town on the banks of a river. _M. decumanus_ cannot be tamed and in captivity soon dies as a rule. _Mus rattus_, with its variety _Mus alexandrinus rufus_, prefers to live on upper floors, roofs, and sometimes the branches of climbing plants. These are easily tamed and live, but will not breed, in captivity. Rats were found by Thompson (1906) to breed the year round, but probably a little less freely in the four colder months in Sydney. Rats eat each other in nature;

rather more than 8 per cent. of the carcases brought in were observed by Thompson to have been partly devoured, but sometimes so completely that nothing but the head, paws, tail, and skin remained. It was found that rats eat mice in nature as well. The progress of the disease among the horde infecting any premises has been usually quite slow. Although, for some unknown reason, plague occasionally sweeps off the entire horde, it very much more often follows a slow course in buildings, and when it does so the horde does not become alarmed, or leave the premises.

(5) Though mice of all kinds are very susceptible in the laboratory to plague, there is little evidence that they suffer from it to any extent under natural conditions.

(6) The sylvatic plague committee (loc. cit.) lists the following rodents under the Muridae as suffering from spontaneous plague.

Muridae

| | |
|---|---|
| Gilbert white-footed mouse | _Peromyscus truei gilberti_ (California) |
| Western bushy-tailed wood rat | _Neotoma cinerea occidentalis_ |
| Intermediate wood rat | _Neotoma lepida intermedia_ |
| Dusky-footed wood rat | _Neotoma fuscipes_ |

c. Family Sciuridae

(1) Plague in the ground squirrel is a disease that is readily recognized by the gross anatomical changes it produces. The commonest lesion, and often the only one, is a

bubo. In many cases the bacilli found in squirrels are highly virulent for guinea pigs and white rats, in other cases the virulence is somewhat reduced. The cervical, axillary, and pelvic glands are easily distinguished, being found in the usual situation of these glands in other rodents. The inguinal glands are easily distinguished, being found in the usual situation of these glands in other rodents. The inguinal glands are located somewhat differently. In the squirrel there is a lymph node lying immediately above the pelvis on each side and very near the middle line. In addition to this gland, which has been called the median inguinal gland, there is a chain of glands lying rather far back in the groin, sometimes extending nearly to the vertebral column. These have been called the posterior inguinal glands. The lesions of plague in ground squirrels resemble more closely the changes found in the plague in guinea pigs than those present in rats and mice. They present a wider variation than those found in other animals.

(2) The survery studies made throughout the western states since 1908 and particularly since 1934 by the Sylvatic Plague Committee (1937) proved that the rodents listed in the table following suffer from spontaneous plague.

Rodents that suffer from spontaneous plague

Sciuridae

| | |
|---|---|
| Beecheyi ground squirrel | _Citellus beecheyi_ |
| Oregon squirrel | _Citellus oregonus_ |

| | |
|---|---|
| Utah spermophile | Citellus armatus (Nevada and Idaho) |
| Rock squirrel | Citellus grammurus (Utah) |
| Columbia squirrel | Citellus columbianus (Oregon) |
| Richardson squirrel | Citellus richardsonii (Montana) |
| Yellow-bellied marmot | Marmota flaviventris englehardti (Utah) |
| Tahoe Chipmunk | Eutamias quadrivittatus frater (Allen) |
| Utah prarie dog | Cynomys parvidens |

(3) The ground squirrels (Arctomyinae) and the tree squirrels (Sciurinae) are numerous, diversified, and widely distributed in North America. Plague among these animals is known elsewhere in the world. Ranchers have observed that, especially in harvest time, norway rats (Mus norvegicus) emigrate into the fields and then may be seen running in and out of ground squirrel holes.

(4) Clemow (1900) states that in the Transbaikal province in Eastern Siberia, a marmot known as the Tarbagan (Arctomys bobac) suffers at time from a disease believed to be plague, and that this disease is occasionally transmitted to human beings. In an endemic plague center in Eastern Mongolia there is also some evidence that these animals contract the disease.

d. Family Geomyidae

Gophers (Thomomys bottae) are said by McCoy (1909a) to be highly resistant to plague when inoculated by the cutaneous method, but apparently often susceptible when inoculated subcutaneously. As only four animals were used for the

subcutaneous inoculation, no sure conclusions can be drawn from the experiments.

4. Order Ferae

a. Family Felidae

Simpson (1905) and DeSouza, Arruda and Pinto (1910) believe that cats can be infected with plague.

B. Class Aves

It is generally concluded by a number of investigators that birds; namely, pigeons, ducks, turkeys, and chickens are not susceptible to plague.

# CHAPTER V

## THEORIES OF THE TRANSMISSION OF PLAGUE

### A. DIRECT CONTAGION FROM MAN TO MAN

Many instances have been recorded in which persons incubating or sick with plague have taken the infection into distant villages and localities, thereby setting up a new locality for the disease. The pneumonic and septicemic varieties of plague are the most dangerous for this means of dissemination. There are also recorded many instances in which doctors, nurses, and relatives have been taken ill with plague through the infection of plague patients.

### B. THROUGH SLIGHT ABRASIONS OF THE SKIN

The fact that primary buboes occur so very often in the inguinal and axillary regions in cases of plague it is believed that the skin is the most common place of entrance of the bacillus into the human body. There are a large number of cases in which medical men have contracted plague through a wound or abrasion in their hand which has been infected while they were performing a post-mortem on a plague case.

### C. THROUGH THE ALIMENTARY TRACT

Some physicians, because of the few instances in which it is possible to trace the place of the infection to the skin, believe that the primary site of infection is through the alimentary canal.

### D. THROUGH THE RESPIRATORY TRACT

The local infection of the nostrils, pharynx, or mouth may extend into the lungs and set up the pneumonic form of plague, or the bacillus may gain an entrance direct into the lungs by the inspiration of infected material producing bronchitis. Cases are not infrequent in which laboratory assistants and other workers have become infected in this manner.

### E. THROUGH INFECTED CLOTHES, SOIL, OR HOUSES

Many outbreaks of plague in homes have been attributed to the introduction of plague infected clothes into the home. Rosenau (1901) found that clothing and bedding were especially likely to be contaminated with sputum and the discharges from buboes and blisters. It was shown that infected clothing may harbor the bacillus for months.

As previously stated the early report of Yersin (1897) that he had found organisms closely resembling _Bacillus pestis_ in the earth of infected localities led to the investigation of the saprophytic existence of _B. pestis_ in the soil. It was seen that cow-dung floors may remain infective for 48 hours but no longer, and that chunam floors do not remain infective even for 24 hours.

### F. THROUGH THE BITES OF INSECTS

Insects have at various times come under suspicion of

being either active or passive agents in the dissemination of plague. Hunter (1906) says if an insect comes in contact with microrganisms of an infectious nature, the latter may be deposited, either on the surface of the body of the insect, e.g. the wings and feet, or in the alimentary canal of the insect. Further, that it must be admitted that such a deposition is an every day occurrence. The bodies and appendages of insects are covered with bacteria of all kinds, the nature of the latter being dependent upon the surroundings.

a. Bonardiere and Xanthopulides (1902) believe that the mosquito plays no small part in the transmission of Bacillus pestis especially in warm countries where they breed during all the seasons. This statement is based on the fact that these observers found B. pestis to be present in the alimentary tract of a mosquito found in the room of a plague patient. Hunter (1906) examined about 20 to 30 mosquitoes each of Culex and Anopheles but did not find any B. pestis to be present.

b. Yersin (1894), Herzog (1905), and Hunter (1906) have on different occasions found Bacillus pestis to be present in or on the alimentary tract and feces of flies which have been taken from rooms in which there were plague patients. A guinea pig inoculated by Yersin with the legs, wings, and head of a fly ground in bouillon died in 48 hours with the specific lesions of plague. Hunter reports that plague bacilli remain virulent for 48 hours or more in the

intestines of flies.

2. Nuttall (1899) found that Bacillus pestis dies off rapidly after being 24 hours in the stomach of bed-bugs, all being dead after 5 days. Negative results were obtained by Nuttall in his effort to infect mice with 22 bugs which had sucked the blood of a mouse dying of plague. Herzog (1905) demonstrated the presence of B. pestis in Pediculi taken from the scalp of a nine to ten year old girl who had plague. Hunter (1906) found B. pestis in the feces of bugs. Bacot (1915) states that for a percentage of bugs (Cimex lectularius) and probably all newly hatched ones, a meal of septicemic blood from a mouse dying of plague is fatal. He further states that bugs which are not killed by the infecting meal are capable of carrying B. pestis and reinfecting mice after a period of 48 days' starvation.

3. Hankin (1897) found that ants neither die of the disease nor retain the infection for any length of time. In some cases ants, from localities in which rats were actually dying of plague, were found to be infected. On the other hand, however, localities in which a severe epidemic was going on among human beings but in which there was no evidence of the death of the rats, ants were always found to be free of the infection. In India ants will eat up a rat dead of plague with extraordinary rapidity, and it cannot be denied by thus disturbing and carrying about infected material they may increase the risk of infection from dead

rats.

4. Cockroaches have been found by Hunter (1906) to contain Bacillus pestis in their feces. No evidence was found to indicate that these insects were materially affected by the presence of B. pestis in their alimentary canals. These results show that there is a great possibility of micro-organisms finding refuge in the body of an insect where it may possibly multiply indefinitely, and, by way of feces, distribute its progeny over wide areas.

5. Simond (1898) presented the idea of the transmission of plague by insects. Simond states that the mechanism of the propagation of plague includes the transportation of the virus by the rat and man; and from rat to man by parasites.

This work by Simond was severely criticized by Nuttall (1902), Noc (1905), Galli-Valerio (1900) and many others. The most serious objections to Simond's hypothesis are: (1) the experiments were not confirmed by any other investigators and (2) in these experiments Simond did not keep an account of the species of fleas which parasitize rats, nor of the inclination of these species to attack man, nor even of their relationship to those species which do not parasitize man. The nature and results of the later experiments performed to confirm the work of Simond will be discussed in detail.

# CHAPTER VI

# THE GENERAL CHARACTERISTICS OF FLEAS

## A. THE CLASSIFICATION OF FLEAS

### Synopsis of families[1]

A. Thoracic segments strongly shortened and constricted; labial palpi without pseudo-joints; third joint of antennae without completely separated pseudo-joints.
  - B. Maxillae without or with very short and broad projecting laminae, their palpi extending beyond anterior coxae; head strongly angulated anteriorly in both sexes; metathoracic epiphyses extending over nearly two or even three abdominal segments; the female becoming endoparasitic when gravid, with globose, enormously dilated abdomen, in which the original chitinous sclerites are mostly obliterated. Rhynchoprionidae
  - BB. Maxillae with a long, narrow, curved lamina which projects downward and backward, their palpi equaling the anterior coxae, or shorter; head evenly rounded in both sexes; metathoracic epiphyses extending over but one abdominal segment; gravid female with abdomen vermiform...... Hectopsyllidae

AA. Thoracic segments not strongly shortened and constricted, their epiphyses extending over but one abdominal segment; labial palpi with three or more pseudo-joints; maxillary palpi almost always shorter than anterior coxae; third joint of antennae with nine more or less distinctly separated pseudo-joints.
  - B. Fifth tarsal joint broadly dilated and greatly lengthened beyond the fourth pair of lateral spines; fore tibiae armed on posterior border, very large black teeth or a few heavy spines; fifth tarsal article on forelegs as long as rest of tarsus, on all the legs with the claws nearly as long as the fifth joint; fore coxae nearly nude, with but few long spines........................ Malacopsyllidae
  - BB. Fifth tarsal joint never greatly enlarged, never as long as the rest of tarsus, the claws shorter;

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[1]Baker, Carl F., 1906. The Classification of the American Siphonaptera. Proc. U.S. Nat. Mus., Vol. 29, pp. 123 and 124.

tibiae armed on posterior border with slender spines; fore coxae always clothed on outer side with several to numerous oblique rows of bristles.

C. Gena with a large recurved process on lower margin extended downward and backward; labial palpus five-jointed; mandibles not distinctly serrate; maxillae long, rather narrow, and obtuse at apex; eye distinct; ctenidia absent; antepygidial bristles absent; anal style of female absent............................ Lycopsyllidae

CC. Gena never with a recurved process; mandibles usually distinctly serrate; anal style present in female.

D. Maxillae triangular, acute at apex.

E. Posterior tibial spines in pairs and few in number, not in a very close-set row...Pulicidae

EE. Posterior tibial spines numerous, mostly single and in a close-set row...Ctenopsyllidae

EEE. Posterior tibial spines in numerous, short close-set transverse rows on posterior border with about four spines in each row... Hystrichopsyllidae

DD. Maxillae clavate or subquadrangular; face strongly sloping forward and recurved just above the mouth, where there are two tooth-like plates on each side; eyes absent; pronotum and usually abdomen with ctenidia; confined to bats.......................... Ceratopsyllidae

## B. EXTERNAL STRUCTURE OF THE FLEA[1]

1. The body in the Siphonaptera is laterally compressed thus making it easy for the insect to work its way through the hair or feathers of its host. Compression is limited mainly to the thorax and abdomen. The common fleas vary in size from 1.5 to 7 mm. in length according to the species; there is comparatively little variation in size within a given species. Dolichopsylls stylosus is the largest flea known. The males are as a rule smaller than the females. The body of the flea is divided into three parts; the head, thorax, and abdomen. The segments are distinct from one another except in the head, and are arranged in a simple manner, one tergite and one sternite to each segment as a rule.

2. The exoskeleton is composed of a chitinous cuticle which varies in hardness and thickness on various parts of the body. The epidermis or true skin is located just beneath the exoskeleton. The chitinous exoskeleton is secreted by an outer layer of cells on the insect's body. This chitinous deposit is thinner at the joints than on the plates. The absence of carbonate and phosphate in the chitin makes it much lighter than that of the lobster. Chitin is structureless in that it does not consist of cells. It is very durable and resists boiling in acids or alkalies. The color of the exoskeleton varies from a pale or light yellow to a ruddy or

[1]References for structure: Patton and Cragg, 1913; Russell (1913); and Herms, 1923.

dark brown. The exoskeleton is sprinkled over with spines, bristles or hairs, directed backward so as not to impede progress. The arrangement on the body, the size, and the presence or absence of these bristles serve as a basis for distinguishing different species. These bristles are not always the same in arrangement and size in the two sexes of the same species. Usually the males have more bristles than the females. There are backward-extending spines on the posterior edges of the abdominal segments to prevent the backward motion through the hair of the host.

3. The head is slightly flattened laterally, rounded on the top and front and shows no obvious trace of segmentation. Patton and Cragg (1913) describe the head as being triangular in appearance when viewed from the side; the dorsal body being rounded from the dorsal and posterior angle to the distal ventral one. The posterior body which is mainly vertical, though with a small tubercle projecting backward in its upper part, articulates with the prothorax without the intervention of a neck. The ventral border is straight, and is armed with a row of stout and heavily pigmented spines, projecting well beyond the margin, and directed downwards and backwards. These spines constitute the genal comb, sometimes called ctenidia. The lateral area of the head on each side is divided into two portions, known as the frons and occiput, respectively, by the antennal groove which runs from the middle of the ventral border

upwards and forward. The thorax itself is composed of three distinct segments. The joints between the segments of the thorax allow a certain amount of movement. Each of the segments consists of a tergite which is undivided and simple and a sternite which is fused more or less closely with certain sclerites representing the pleural plates as described in Diptera.

a. The eye is situated anterior to the middle groove. It is non-facetted, and is conspicuous on account of its dense pigmentation. In many fleas the eye is absent or vestigial. The mouse-flea (Leptopsylla musculi) and the bat-fleas (Ceratopsyllidae) are blind. In blind fleas there is often a spine where the eye should be. In one genus both the eye and the spine are present. In another species the spine is rudimentary and there is some black pigment beneath it. It is generally believed by entomologists that the power of vision of ocelli is probably confined to very near objects and that this simple form of eye is more useful in dark places than the compound eyes. It is sufficient that the eye of the flea perceives from which point the light comes so that it can escape in the opposite direction.

b. Fleas keep in touch with each other and with their surroundings by their antennae. The antennae of fleas; unlike those of a moth, beetle, or grasshopper, fit into a groove at the side of the head and can be protruded when desired. This enables the insect to move swiftly through the

hairs or feathers of the host. The antennae consist of three joints of which the distal one, known as the club, is the largest, and especially modified.

c. The mouthparts of the flea are adapted for sucking and piercing. The mouthparts project downwards and in some fleas as the Pulicidae a little backwards, from the distal portion of the head. The proximal ends of the mouthparts are concelaed by the genal comb in the cat flea and its allies. The mouthparts project from an opening in the head cavity which is surrounded by a thinner layer of chitin. This opening is sometimes called the peri-oral ring. The maxillary palps lie in front projecting from the front of the head like antennae. The labium lies behind the maxillae and usually ensheaths them.

(1) The labrum-epipharynx is a long and slender organ, presenting a rounded contour on section, but flattened on its ventral surface where it is in opposition with the mandibles. Its dorsal wall, corresponding to the epipharynx, is composed of rigid yellow chitin, while the lateral walls which connect these parts are more membraneous. Within these walls there is a space continuous with the haematocoele of the head, and limited distally by the fusion of the two parts. The labrum extends to the distal extremity, the two parts taking about an equal share in the formation of the compound eyes. The lateral edge of the labrum bears fourteen pairs of forwardly directed tubercles of extremely small size. These

are probably sensory organs as a central canal can be distinguished in them under a high magnification. Proximally the chitinous portion of the labrum ceases at the peri-oral ring, to the margin of which it is attached by a narrow band of membraneous chitin. The epipharynx, or ventral lamina of the compound organs, has no attachment to the wall of the head cavity, but is continued inwards in direct chitinous continuity with the dorsal wall of the pumping organ. The distal end of the labrum-epipharynx is blunt and rounded, and is not provided with teeth or tubercles.

(2) The hypopharynx is rudimentary and can be seen only in dissections. It consists of a small, thick triangular plate, continuous behind with the salivary receptacle, and projecting forward between the epipharynx and the mandibles at the base of the proboscis. It is pierced through the center by the salivary duct, which opens at its pointed apex, permitting the saliva to flow into the grooves of the mandibles immediately distal to it.

(3) The mandibles are the most important of the mouthparts because they are the only cutting weapons. They take part in the formation of the food canal, and convey the saliva to the wound. Each mandible is a broad blade, rounded in contour, at the proximal end, but flattened for the greater part of its length, the surfaces of the two blades being inclined backwards and inward from the external border. At the proximal end the internal surfaces are in contact with the

hypopharynx, but where this short piece ceases they come to lie in contact with the epipharynx, forming the lateral sides of the food canal; from this point the flattened blades are inclined more vertically. On the inner side of each mandible there is a groove, beginning at the point where the hypopharynx ceases, and narrowing as it proceeds distally, until in the distal half of the blade it is almost closed by the approximations of its edges. The groove receives the saliva from the canal in the hypopharynx, and conveys it to the distal end of the proboscis. The distal two-thirds of the extreme surface of the mandible has minute hook-like teeth, arranged in three or four rows, and directed towards the base of the blade. The purpose of this membraneous expansion is to ensure that the canal formed by the mandibles and epipharynx shall be tightly closed during the act of sucking. The mandibles articulate to the wall of the head capsule by a second joint at its proximal end. This joint consists of a stout, rounded rod of chitin, attached to the base of the blade by its exposed distal end. Patton and Cragg (1913) describe the action of the mandibles as follows:

> "The internal rod, which corresponds to the cardo, rotates on the articulation between the tubercle and the pit in which it lies, the two forming a single cup and ball joint. The excursion will be at least through a right angle, and as the distal end passes forward it carries with it the blade, which is thus protracted through the wound".[1]

(4) The first maxillae of the fleas are not cutting

[1]Patton and Cragg, 1913. A Textbook of Medical Entomology. London: Christian Literature Society for India, p. 440.

organs, and probably do not enter the wound. They lie in a plane anterior but external to that of the mandibles. The labium is the most posterior of the mouthparts, and consists of two lateral portions, usually called the labial palps, united basally to a median piece. The labium and labial palps form what is called the rostrum; the number of joints of which it consists is an important fact in classification. The paired portions of the labium are slender jointed organs, each consisting of four segments.

4. The sclerites are much more regularly arranged in the abdomen than in the thorax. The abdomen is made up of ten pairs of sclerites in all, the last three being modified for sexual purposes.

5. The spiracles of the flea are regularly arranged. There are three in the thorax and one between each of the abdominal segments from the second to the ninth. The spiracles lie in the soft portion of the tergite, above the middle line of the lateral surface. That of the first abdominal segment lies between the tergite and the epimerum of the metathorax. The spiracular openings are enclosed by rings of chitin, and are easily recognized in cleared preparations.

6. The hairs or bristles for the most part are arranged in regular rows, one to each segment. The rows are not placed terminally, but in the middle of the chitinous plate where the chitin is thickest. There are two rows on the epimerum of the metathorax, and two on the first abdominal

tergite. The small eminences of the ninth tergite in front of and below the claspers bear tufts of hairs. The bristles or bristle at the dorsal angle of the seventh segment is called the antipygidial bristle. The number of these bristles and the number of hairs on the joints of the legs, and particularly the presence of the tufts on the femora and coxae are important taxonomically.

## C. INTERNAL ANATOMY OF THE FLEA[1]

1. The internal anatomy of the flea is fairly simple. The digestive canal is a slender tube connecting the mouth and anus. It is less convoluted and straighter than that of the higher vertebrates. This canal passes through the middle of the flea's body and is kept in position partly by muscles and partly by numerous branching tubes through which the insects breathe. Above the digestive canal lies the heart and beneath it the nerve cord or chain of ganglia. The mouth opens into the pharynx, a chitinous chamber dorsal to the antennae in the head. The pharynx is somewhat elongate, but is expanded more on the dorsal than on the ventral side. It consists of a dorsal and ventral chitinous plate. The dorsal plate is continuous with the epipharynx and the ventral with the hypopharynx. In the case of the hypopharynx

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[1]Reference for structure: Patton and Cragg, 1913 and Russell, 1923.

the chitinous portion of the two laminae are separated by a layer of fibrous tissue in which the salivary duct lies. Posteriorly the pharynx tapers off at the hind portion of the head to become continuous with the esophagus. The dilator muscles are separated into several bundles and pass between the dorsal plate and the wall of the head cavity. When these muscles contract and relax in regular sequence, a rhythmic action of the pharynx itself occurs and a steady stream of blood is forced or drawn from the mouth stomachwards.

a. The esophagus is very thin, the wall consisting almost entirely of very thin and flexible chitin, with few cells and no muscular tissue. The esophagus extends as far as the posterior limit of the thorax.

b. The proventriculus is a short conical or button-shaped body, situated between the esophagus, the posterior end of which is dilated at the point of junction, and the midgut. A close-set series of long chitinous rods arise from its inner surface. These processes act as an effective valve preventing the regurgitation of the contents of the gut when the pharynx is dilated in the act of sucking, and to compensate thereby for the lack of muscles in the wall of the esophagus. During the life of the flea the stomach is constantly churning its contents. Some valvular arrangement between the stomach and pharynx would seem to be nearly essential. In many cases fleas will feed when the stomach is already full of blood and some sort of valve is needed to prevent

regurgitation into the pharynx when the pharyngeal muscles contract and the walls of the pharynx contract, the negative pressure so produced closes the lumen of the proventriculus by drawing the rods in contact with one another. The wall of the proventriculus itself has no muscular tissue.

c. The midgut or stomach is the largest part of the alimentary tract. It is an elongate, oval body extending to the hind end of the body. The walls of the midgut are made up of muscle fibers, more irregularly arranged than is usually the case, and not separable into definite longitudinal and circular bands, and internal to this is a single layer of cells set on a basement membrane. The cells are cubical or columnar, and appear quite irregular in outline in most sections because some of the cells are in the act of discharging their secretions into the lumen of the gut, while others have emptied themselves and are degenerating. Blood in all stages of digestion is often seen in fleas dissected shortly after removal from the host. Russell (1913) states that the average capacity of a rat-flea's stomach has been estimated to be half a cubic millimetre.

d. The hind-gut is narrow, and is rather shorter than the midgut. It lies curled in the posterior part of the abdomen, and dilates distally to form a pear-shaped rectum, in which there are six rectal papillae similar to those of Diptera. The function of the rectal papillae seems not to be known. There are four Malpighian tubes, which enter the gut

at the posterior end of the stomach by separate openings.

e. There are two pairs of salivary glands on each side of the anterior end of the flea's stomach. Each pair gives off fine ducts which unite after a short course to form a common duct, the common duct of the two sides uniting in the neck and passing to the salivary receptacle just behind the hypopharynx. Each gland is rounded or slightly oval, with the narrow end directed forward, and is composed of a single layer of comparatively large cells arranged around a central lumen. A spiral chitinous membrane lines the common duct and distal portion of the duct of each gland to prevent the collapse of the tube when the saliva is drawn forwards by suction. The salivary pump lies below the anterior portion of the pharynx, and consists of a small chitinous chamber. A series of dilator muscles are attached to the walls of the chamber. These act by drawing the walls of the pump apart so as to suck up the saliva from the glands by means of induced negative pressure. The salivary pump receives saliva from the glands by means of the two salivary ducts. The saliva is propelled through the exit-duct of the pump into the salivary canal in the mandibles. The opening of the exit-duct is adjusted so as to be opposite to the canals which extend down the mandibles like troughs. It would seem that when the flea is feeding, saliva is pumped into the puncture and blood is pumped out.

2. The male organs of reproduction consist of a pair

of rather large testes, spindle-shaped and pointed at both ends; an extremely fine efferent duct from each; and a complex penis. A common sheath of fibrous and muscular tissue surrounds the posterior portions of the vasa deferentia so that there appears to be only one common duct, but there are two ducts and these do not unite until they reach the base of the penis sheath. At this point there is a small pouch of an irregular shape, consisting of two horizontal links united by a vertical one. The two ducts from the testes open into the seminal receptacle by a common opening, while the common ejaculatory duct leaves its posterior side at the angle between the posterior transverse limb and the vertical one. The penis and its sheath constitute an exceedingly complex sexual organ.

a. The ovaries consist of eight ovarian tubes on each side, leading to a short common duct which opens just ventral to the anus. The spermatheca is a small U-shaped chitinous pouch, which, like the male sexual organ, becomes conspicuous when the soft tissues are dissolved out of the body of the flea. The shape and size of the pouch vary in different species, and are sometimes used as points of distinction. Each ovariole when mature, consists of a long tube which tapers gradually from base to apex. The lower portion is divided into a series of follicles, usually three or four. Of these the lowest contains a mature egg, while the next two or three contain nurse cells and ova of approximately the

same size as one another. The remainder of the tube is filled up with a large number of young ova diminishing in size and degree of maturation from the base upwards and in a gradual manner. The lowest seven to ten of these are a little less in width than the tube in which they lie, and are partly separated from one another at the sides, though the marginal epithelium is not developed. Higher up the ova are smaller and are more crowded together, and higher still they diminish rapidly in size until they form a crowded mass of cells at the upper part of the tube. As many as twenty ova can be distinguished in some of the ovarioles. All the ovarian tubes in the same flea are not in the same degree of development, and even when the abdomen is obviously distended and the flea about to oviposit one finds some of the ovarian tubes in an immature condition.

3. The organs of respiration in a flea consist of stigmata which open into the trachea. The flea has more stigmata than any other insect. The trachea is subdivided into a number of smaller branches which supply the adjacent tissues. The blood of the flea is almost colorless and is without red corpuscles. The heart of the flea is a very delicate pulsating tube which lies along the back, above the digestive canal and immediately beneath the integument. There is no closed system of arteries, capillaries, and veins such as exists in higher organisms. The blood circulates in the cavity which exists between the body wall and the various

internal organs.

4. The nervous system of the flea is not very well developed and shows little differentiation. The brain consists of two lateral masses, corresponding to the supra-esophageal ganglia, which are united to one another by a broad commissure, and two almost equally large ganglia below and behind them, the sub-esophageal ganglia; the two pairs of ganglia are united by commissures which enclose the esophagus. There are three thoracic ganglia which are distinct from one another and are approximately equal in size. There are seven abdominal ganglia, all equal in size except the last, which is the largest of the abdominal ganglia. Both the thoracic and abdominal ganglia show evidence of being composed of two lateral halves. This primitive condition of the nervous system is a strong argument against fleas having had winged ancestors.

# CHAPTER VII

# THE LIFE HISTORY OF FLEAS

Most observations in regard to the life history of fleas have been made on those fleas which are connected with rats and plague. The life history of fleas includes four distinct stages: egg, larva, pupa, and adult. The adult flea which has just emerged from the pupal case is called an imago by several investigators. This type of development is known as complete metamorphosis.

## A. THE BREEDING PLACES OF FLEAS

The breeding places of the different species of fleas vary with the habits of their hosts. Birds' nests are the breeding places of fleas found on birds; human habitations, the breeding place of *Pulex irritans*, and in the case of rats the breeding places of their fleas vary with the habits of the species of rat: thus, those fleas found on *Mus decumanus* breed in the burrows made by this rat, those on *Mus rattus* breed in all sorts of situations which afford a shelter to these animals.

## B. EFFECTS OF CLIMATIC CONDITIONS ON BREEDING

Many experiments have been performed by various investigators in an effort to determine the effects of lack of food, temperature, and general climatic conditions on the

breeding of fleas. Mitzmain and his co-workers (1910) concluded from a series of experiments in which as near as possible the conditions found in nature were duplicated, that mammalian blood appears essential to fleas for the performance of the normal functions of copulation and oviposition. They observed that fleas kept constantly in jars and reared from cocoons, never having fed upon a host, did not copulate or oviposit. In 30 specimens of Pulex irritans taken from a house which had been vacant for six weeks they found, after three days' observations that the fleas were perfectly healthy, and although females predominated, no eggs were found at the end of the period. As a control, 6 females of this species collected from human hosts when kept in separate vials laid eggs normally depositing from 5 to 12 in each instance. Mitzmain and his co-workers obtained similar results from four experiments with Ceratophyllus acutus, the squirrel flea. When reared from cocoons and kept starved in jars at room temperature, this species too did not mate or lay eggs. It was further observed that when fertile females were kept under artificial conditions the eggs were laid in one laying in a period beginning two hours after copulation and extending to a maximum of thirty-six hours. It was also noticed that when deprived of food the female does not oviposit after this length of time.

The results of the experiments of Bacot (1914)

substantiate those of Mitzmain. Most, if not all, the species dealt with in Bacot's experiments were observed to copulate shortly after emergence from the cocoon, but no signs of either eggs or brood were found in any of the boxes, jars, or other receptacles in which unfed fleas were kept. Experiments in specially prepared jars, containing food for any larvae that might result, and also abundant cover for the fleas, gave the same result. On the other hand, virgin fleas of Pulex irritans, when fed, laid freely, though only infertile eggs. In fact, during the course of these experiments, no support whatever was obtained for the theory that flea breeding can take place from one generation to another in the absence of an animal host to provide food for the adult. Bacot says:

> "The experiments in which the opportunities offered to adults of P. irritans to feed were varied afforded no evidence that the amount of food taken had any influence on the fertility of the eggs laid, but only upon the number".[1]

The Advisory Committee (1908) appointed by the Secretary of State, the Royal Society, and The Lister Institute to study plague in India concludes from a series of experiments performed to determine the effect of temperature on the breeding season, that a high mean temperature affects the breeding of fleas to a considerable extent, and

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[1]Bacot, A.W. 1914. A Study of the Binomics of The Common Rat-flea and Other Species Associated With Human Habitations, With Special Reference to The Influence of Temperature and Humidity at Various Periods of The Life History of The Insect. Journ. Hyg., Plague Suppl. III, p. 651.

that it appears not only to restrain the imago from depositing eggs but also to be deleterious to the development of eggs into larvae. There would seem also to be an optimum temperature at which breeding takes place more vigorously than at other temperatures.

## C. THE EGGS

The eggs are deposited by the female flea in places where the host usually sleeps. They may be viscous as in *Pulex irritans*, *Ceratophyllus fasciatus*, *Lycopsylla cheopis*, *Ceratophyllus acutus*; or dry as in the case of *Ctenocephalus canis* and *Ctenocephalus musculi*. The eggs of the former group adhere to the medium on which they are laid, while the eggs of the last two species are laid loosely, so that they roll about when the vial containing them is shaken. Most species deposit dry eggs and hence they do not become attached to the hairs of the host even though oviposition has taken place there. There is every reason to believe that some species of fleas seldom or never deposit their eggs among the hairs of the host, preferring loose earth, excrement, and dust. Large quantities of eggs may be found on sleeping places of the flea hosts. In some of the warmer parts of the world as India, the female flea deposits her eggs the year round. The number of eggs deposited at one laying by different species varies from 3 to 18, the rat fleas averaging 6 and the squirrel fleas as many as 18.

The eggs of the flea are comparatively large (.5mm. long), glistening white and blunt at both ends. The eggs may be deposited either by day or during the night, and are not attached to the surroundings in any way, but simply dropped on the ground or bedding near the host. Comparatively few eggs are deposited at any one time. It is very seldom that a female deposits her eggs in a tube where they may be counted.

## D. EFFECTS OF CLIMATIC CONDITIONS AND LACK OF FOOD ON THE NUMBER OF EGGS LAID

Climatic conditions, lack of food, and temperature have definite effects upon the number of eggs laid as is shown by the experiments of Bacot, Mitzmain, and the Advisory Committee.

Bacot (1914) states that in the case of both *Pulex irritans* and *Ceratophyllus fasciatus* it is possible to induce them to lay at any time by placing them in a warm, moist atmosphere (23.88 degrees C., humidity about 70%). While *Pulex irritans* is the more responsive of the two, in neither case do the number of eggs laid under these conditions reach the summer average. With *Xenopsylla cheopis* the response to incubator treatment during the winter months is but slight; very few ova are obtained by removing females from the cages and placing them in an incubator at 23.88 degrees C. for 24 hours. It appears necessary for egg production by this species that their host should be living in a warm atmosphere. Bacot further states that *Ceratophyllus canis* also, under

suitable conditions, lays during the non-breeding season and that _Ceratophyllus gallinae_ is probably more fixed in seasonal habit than the other species as regards egg laying.

Mitzmain and his co-workers (1910) further observed that eggs may be deposited while the insect is still under the influence of an anesthetic, when covered by a glass slip, and when exposed to a strong sunlight.

The Advisory Committee (1912) concludes from their experiments concerning the number of eggs laid as influenced by climatic conditions that in the presence of moisture, especially in the drier months of the year, a distinctly larger number of eggs were laid by the fleas. Their results show that temperature has a marked effect on the number of eggs laid. Room temperatures of from 24 degrees C. to 28 degrees C. are the most favorable for egg laying. At higher and lower temperatures fewer eggs were laid.

## E. EFFECTS OF TEMPERATURE AND HUMIDITY UPON THE TIME NECESSARY FOR EGGS TO HATCH

Herms (1923) states that high mean temperature from 35 degrees C. to 37 degrees C. inhibits development, which may account for the fact that the eggs do not hatch well on the host.

The Advisory Committee (1912) performed a series of experiments to find out the effects of varying temperature and varying humidity on the hatching of flea eggs. Their

experiments and results may be described as follows: Test tubes in which fleas' eggs had been deposited were placed, some in a dark box and others in an ordinary well-lighted room, but not in direct sunlight, in order to determine if the number of eggs hatched was in nature affected by daylight, as well as to ascertain the number of eggs hatched at different seasons of the year. Out of 5543 flea-eggs kept in a light room and 5571 kept in a dark room, the percentages hatched into larvae were 32.6 and 32.9 respectively. It appears that with certain limits of temperature, there is a distinct correlation between the number of eggs hatched at different seasons of the year and the percentage of atmospheric humidity.

Results show that the artificial raising of the humidity was distinctly favorable during the naturally dry months; but the difference was not so marked, indeed it was occasionally less favorable in the months of the rainy season, especially in June and August in India. Artificial lowering of the humidity on the other hand was distinctly unfavorable in the dry season, when the atmospheric humidity was already very low. In the rainy season with this lowered humidity there was still a marked difference, except in the month of August (in India) when sufficient humidity was apparently not removed to interfere with the process of egg hatching. It was noted that when the humidity was exceptionally high, moulds formed readily in the breeding receptacles, especially on the eggs, from which their mycelia could be seen radiating in every direction, and it is

possible that these may have killed the eggs. It will be noticed that in the month of August when the average humidity (85.5%) was considerably higher than in any of the other months, fewer eggs were hatched under ordinary atmospheric conditions than there were during June, July, and September. Moreover by further raising the humidity during this month the number of eggs hatched fell still further, that is, from 28.6% to 20%.

Experiments show that the seasonal changes in egg laying and in egg hatching run together with the result that more than twenty times as many larvae were obtained in September and October, when it was warm and wet, than in April and May, when it was hot and dry.

Mitzmain (1910) found that the egg stage lasted from 7 to 9 days at a temperature from 17 degrees C. to 23 degrees C., and about 14 days from 11 degrees to 15 degrees C.

Strickland (1908) states that the egg hatches after a relatively short incubation period (5 to 14 days), the duration of which depends mainly upon the degree of humidity. The incubation period is never abnormally prolonged, as in the case of lice, and varying conditions of temperature and humidity have practically no effects on the percentage of eggs which ultimately hatch.

### F. THE HATCHING OF THE EGG

The first signs of egg hatching as described by Mitzmain (1910) are usually recognized by the rising and fall-

ing of the exochorion (outer shell layer) on one side of the shell. The movement becomes more extensive while at the same time the pulsations become quite pronounced, causing the egg to shift slightly from its position. Later a small gash is made on one side of the egg by the egg opener, a wedge-shaped, horny, claw-like structure on the dorsal side, back of the head of the embryo. The first gash increases slowly in length, encircling the egg within an hour. In the course of a few hours seven successive gashes are made. The location of these is quite constant--two on each side of the egg and three at the center, the middle of the central ones being the most distinct. When the last slit encircles the shell the embryo is at the most active stage; it effects a complete rotation in its shell at intervals of ten minutes. The gashes make the shell appear as though cut to ribbons.

The pressure of the body against the shell forms a nearly round hole through which the larva eventually emerges. The opening is enlarged by pressure of the load against the tail, raising the body like a hoop, causing an arch or hump to appear with dorsal side outward.

The amnion sheds slowly on either side from the middle of the arched abdomen ventrally, and with a movement of fluid beneath, it cracks across the abdomen. With a final vigorous bubbling and wrinkling the amnion sheds off, the moulted skin falling on either side, exposing the quite colorless cuticle of the young insect, roughly wrinkled and bristling with

slender hairs or setae. These hairs which are at first transparent turn grayish when exposed to the air. In a few minutes the larva has fully emerged.

## G. FOOD AND DESCRIPTION OF THE LARVA

The necessary conditions of warmth and humidity are provided by the host's body while the provisions of bedding and careful choice of a dry situation all fit in with the needs of the larval stage of the parasite. When the host leaves its nest or lair the temperature and humidity fall together, but, so far as observations have been made, a fall in temperature will only have the effect of retarding the development of the larva; a low humidity, however, if prolonged, is fatal even when accompanied by a low temperature.

The time necessary for the development of the larva into a pupa likewise depends upon temperature and humidity. Bacot (1914) concludes from his experiments that the time occupied by the active larval period is subject to very wide variations, ranging from 15 to 114 days for Ceratophyllus fasciatus, 9 to 202 days for Pulex irritans, 12 to 84 days for Xenopsylla cheopis, and 11 to 142 days for Ctenocephalus canis.

Strickland (1914) concludes that the most favorable conditions for the larva are a low temperature and a high degree of humidity; further, the presence of rubbish, in which the larva may bury itself, is essential to its successful development. The larva is very susceptible to external conditions

and is not very hardy.

After the larva hatches it begins to look for food. At the time of birth a supply of food is found upon the egg shell. Here the larva feeds at first upon the tiny blood pellicles surrounding the egg shell; this the mother furnishes when the egg is laid. When this supply has vanished the larva begins to forage for other food. The larva feeds on the ejecta of adult fleas.

Patton and Cragg (1913) states that in a large proportion of the larvae they examined the intestine contained blood, in stages varying from fresh unclotted blood to particles of blood pigment, the dark color of the living larvae being due to the presence of this material. As the larvae have no biting mouthparts, the most probable source of the blood is the adult flea. It is well known that the flea, like most sucking insects, has the habit of defecating while feeding, or shortly after; not only is the hindgut emptied on these occasions, but fresh blood is passed, the insect appearing to take up more food than it can digest.

Patton and Cragg describe the larva as follows:

> [1]"The larva is a minute maggot-like creature, bearing a strong superficial resemblance to a Dipterous larva. It moves about actively in dust or sand, and is best recognized by shaking up the debris and watching for moving particles, as it usually keeps below the superficial layer. It consists altogether

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[1]Patton and Cragg, 1913. A Textbook of Medical Entomology. London: Christian Literature Society for India, p. 459.

> of fifteen segments, including the head and the hidden terminal segment. Of these the posterior are the largest, the posterior half of the body being distinctly thicker than the anterior, though there is not quite that tapering appearance seen in the Muscid larvae. The segments are rounded, and there are no pseudopodia or legs. The head is small and conical, and bears a pair of simple cylindrical and tapering antennae, at the apices of which there is a minute hair. The base of the antenna is set on a small raised area at the side of the head, dorsal to the mouth, and has around it a row of five or six minute conical and apparently jointed processes. Each of the succeeding segments down to the tenth bears a row of six minute hairs, inserted in the middle of the length of the segment, and increasing progressively though not markedly in length from before backwards, as the segments themselves increase in size. The eleventh and twelfth segments bear eight hairs each; of these the twelfth is the largest of the body, and bears the longest hairs. The thirteenth segment has six hairs, and is considerably smaller than the preceding ones. The fourteenth segment is still smaller, and has on each side a row of four hairs which are rather stouter and longer than the rest, and are placed on the distal margin of the segment. The fifteenth segment is very small, and is concealed by the one in front of it. It bears terminally a row of fifteen minute hairs on each side. Projecting from within the last segment there is a pair of minute slightly curved and elongated pointed processes, arising from a stouter base".

Bacot (1914) states from experiments carried out with Pulex irritans, Xenopsylla cheopis, Ctenocephalus canis, and Ceratophyllus gallinae that there are three larval instars, two of these moults taking place while the larvae are in the active stage--the third skin being cast within the cocoon during the metamorphosis to the pupal condition. The cocoon is described by Bacot as being an oval envelope of silk spun by the larva, its exterior being covered with sand, dust or any small fragments of dry material that are available. These fragments are not worked into the fabric; and it is

probable that the larva collects them and attaches them together with a few silk threads and then proceeds to thicken the interior of this loose case with further accretions of gummy silk from the inside. Not infrequently the cocoon is spun against the side or bottom of the rearing receptacle, the large particles of sand being used in preference to the smaller ones.

The cocoons vary in structure from the flimsy ones of Ceratophyllus fasciatus which are composed of a few silk threads holding together grains of sand or other material, to the more rugged ones of this same species which are strong, hard cases made of a large amount of silk.

Within the cocoon the larva lies doubled into a large loop with some space to spare, although the acute bend in the body suggests discomfort. After pupation there is considerable space unoccupied. There is some doubt as to whether in the different species the extensive periods of rest which occur within the cocoon are larval or imagina. The pupal period appears to be comparatively short, not more than a few days, so far as has been possible to ascertain, and it seems probable that, once the pupal state is entered into, it must be carried to a conclusion without interruption. Resting larvae of Ceratophyllus fasciatus, as well as the pupae of this and other species, have been taken from their cocoons and subsequently produced normal imagines. It is, however, likely that the normal course of development may be

thwarted and a tendency to further rest be curtailed by removal, and it is probable that such disturbed larvae could resist drying as well as other unfavorable conditions.

There seems good reasons to think that the hard, strong types of cocoons commonly made by the larvae of <u>Ceratophyllus</u> <u>fasciatus</u> are associated with the aestivating-hibernating or resting habit; all gradations including the extreme, may be present in the same batch reared under precisely similar conditions. While the evidence is not conslusive that these hard cocoons are always associated with lying over, and the frail ones with prompt emergence, still in a majority of cases this would seem to be the state of affairs. The chance of injury and attack, either by parasites or predatory insects, is certainly lessened by the strength of the cocoon, although it is not easy to see that even the more flimsy cocoons are in much danger of being penetrated by parasites.

A large number of species of fleas have the habit of clinging to a cocoon after emergence and the flea may be overlooked as it sometimes remains quiescent, even after shaking the tube or box in which the cocoons are kept. On the other hand, any disturbance, however slight may be followed by emergence. It is also a fact, that when cocoons are opened for examination, they are found to contain living fleas far too often for it to be reasonably supposed that they are all chance occasions in which the opening has

happened to coincide with emergence. This supports the conclusion that the fleas are normally in the habit of resting, at any rate for a short period, and possibly for many days, before emergence, unless some disturbance gives warning of the approach of a possible host.

# CHAPTER VIII

## THE LENGTH OF LIFE OF FLEAS

### A. WITH AND WITHOUT FOOD

The length of life of the flea with and without food under various conditions is of much importance. The length of life of the mature flea varies with the different species, climatic conditions, and food. During hot, dry weather and when no animals upon which to feed are present, the duration of life may be very short--from 2 to 5 days. When allowed to live on blood they live from a month to almost a year. Bishopp (1921) states that during summer probably the average longevity of the human flea without food is about two months, of the dog flea somewhat less, and of the stick-tight flea still less. The Advisory Committee (1908) reports from a number of experiments in which _Pulex_ _cheopis_ was placed in various materials and the length of time that it was able to live in different surroundings noted, that _P_. _cheopis_ is unable to live for many days in the absence of a liquid food supply. Some of the experiments in which the fleas were placed in a box containing sand with moist cow-dung in one portion, showed that the fleas could survive for a longer period than in conditions in which they did not have access to any moisture. In any case in the absence of their natural food they were not able to live for a fortnight. In another experiment the Advisory

Committee (loc. cit.) found that rat fleas, when supplied with their natural food, the blood of a rat, can live for at least 41 days. When fed on human blood the rat flea can live for 27 days, and when fed on guinea pigs it can live for 20 days.

Nicoll (1912) found that the average length of life of Ceratophyllus fasciatus apart from its host under general circumstances, is just under seven days, but about 9 per cent. live for a fortnight and at least 2 per cent. for three weeks or over (of 505 fleas 46 lived at least fourteen days and 10 at least twenty-one days.). Strickland (1908) states that it is evident that if the adult flea does not obtain food in the form of blood its length of life depends mainly on the nature of its surroundings. In the presence of rubbish in which it can bury itself, the flea may live for many months, whereas in the absence of any such substratum it very rarely lives a month. In the former cases the length of life is influenced to some degree by the temperature and humidity, for in one experiment carried out at 23.88 degrees C. and 45 per cent. humidity, the fleas did not live for more than four months, whilst in another experiment, with an average temperature of 15.55 degrees C. and 70 per cent. humidity, they lived for at least 17 months. A low temperature combined with a high degree of humidity appears, therefore, to be most favorable to the prolongation of the life of the fleas. Mitzmain (1910) found that when used

experimentally the female is invariably longer lived. Experiments to show the length of life with human blood diet show that female fleas of all species outlived the males by several weeks. This is doubtless true under natural conditions, where it was found in collecting fleas from the host that the females predominated markedly.

### B. AS INFLUENCED BY TEMPERATURE AND DRYING

Bacot and Martin (1924) in order to ascertain the separate influences of temperature and drying upon the longevity of fleas with a view to the interpretation of the epidemiological facts, performed experiments as follows: The saturation deficiency was kept constant while the temperature was varied and the temperature kept constant while the saturation deficiency was varied in order to determine the effect of these two variables upon the longevity of the flea. They found that (1) the survival of fleas (_Xenopsylla cheopis_) apart from their host is approximately in inverse proportion to the saturation deficiency of the air, provided the temperature and the air movements are constant. In other words, it is proportional to the rate at which they lose water. (2) under similar conditions but with constant saturation deficiency, their length of life is reduced between one-half and two-thirds by 10 degrees C. rise in temperature. Compared with the effect of saturation deficiency, that of the temperature

upon the longevity of fleas is, within the range of climatic conditions over the greater part of India, a smaller one. (3) A variation in saturation deficiency from 5 mm. to 35 mm. such as occurs in the plains of Northern India at different seasons would, accordingly, shorten the average duration of life of wandering rat fleas in the proportion of 15 to 1. As a rise in mean temperature occurs simultaneously with the increase in saturation deficiency and may amount to a difference of 20 degrees C. between January and June this would reduce the life of wandering fleas to about one-third. The effect of saturation deficiency and increased temperature will be additive and would go a long way to explain some of the climatological features of the epidemics.

C. AS INFLUENCED BY TEMPERATURE AND HUMIDITY

Petrie and Todd (1924) found that (1) for Xenopsylla cheopis, temperatures from 20 degrees C. to 25 degrees C. and vapor pressure deficiencies from 1 to 10 millibars are most suitable for its development at all stages, and (2) that the higher the temperature and the vapor pressure deficiency, a high deficiency indicating excessive dryness of the air, the shorter is the period of survival of adult fleas when they are kept unfed. Experiments of the Advisory Committee (1912) show that the longest life is during August when the humidity is over 80% and their shortest life in April and the first half of May, when the humidity is about 45% or

less. It is of interest to note that in August they were, under the conditions observed in the experiment, found to live about five times longer than they do in April. In other words, plague infected fleas could, under similar conditions, be conveyed five times farther in August than they could be in April. In regard to the effects of varying humidity it is shown that in almost every month, the effect of the addition of moisture prolonged the life of the flea. The contrast was most marked in the month of the hot dry weather. The abstraction of moisture on the other hand, almost always shortened the length of life of a flea. The only exception occurred in the month of February, but this may be accounted for by the fact that the figures were too small to strike an average, as in this month observations were made on five fleas kept in a dry atmosphere. An attempt was made to eliminate the effect of moisture by means of a small piece of photographic drying disc kept in the tubes. The tubes containing the fleas were then kept under varying degrees of temperature. It was seen that the average length of life of the fleas was considerably longer in the low temperature (12.77 to 18.33 degrees C.) than in the room temperature (12.77 to 29.44 degrees C.); in this again it was considerably longer than in the warm temperature 36.66 to 40 degrees C.

# CHAPTER IX

## DIFFERENT FLEAS FOUND ON ANIMALS SUBJECT TO PLAGUE

This list of fleas found on animals subject to plague has been compiled from the reports of the following investigators: Galli-Valerio (1900), Tidswell (1903), Baker (1904), Rothschild (1906), McCoy (1910c), and Chick, Harriette, and Martin (1911).

### Family Canidae

1. *Canis familiaris*, the common dog.
    a. *Ctenocephalus canis* (Curtis) Baker.
    b. *Pulex irritans* Linnaeus.
    c. *Sarcopsylla penetrans* (Linnaeus) Westwood.
    d. *Xestopsylla gallinacea* (Westwood) Baker.

### Family Felidae

1. *Felis domestica*, domestic cat.
    a. *Ctenocephalus canis* (Curtis) Baker.
    b. *Ctenocpehalus felis*.
    c. *Pulex irritans* Linnaeus.
    d. *Sarcopsylla penetrans* (Linnaeus) Westwood.
    e. *Xestopsylla gallinacea* (Westwood) Baker.

### Family Geomyidae

1. *Thomomys bottae*, the gopher.
    a. *Ceratophyllus ignotus* (Baker) Wagner.

## Family Muridae

1. _Mus_ _decumanus_, gray rat.
    a. _Ceratophyllus_ _anisus_ Rothschild.
    b. _Ceratophyllus_ _fasciatus_ (Bosc.).
    c. _Ctenophthalmus_ _agyrtes_ (Heller).
    d. _Ctenopsyllus_ _musculi_ (Duges).
    e. _Xenopsylla_ _cheopis_ (Rothschild).
2. _Mus_ _musculus_, the gray mouse.
    a. _Ceratophyllus_ _fasciatus_ (Bosc.) Curtis.
    b. _Ctenopsyllus_ _musculi_ (Duges) Wagner.
    c. _Ctenopsyllus_ _taschenbergi_ Wagner.
3. _Mus_ _norvegicus_, norway rats.
    a. _Ceratophyllus_ _fasciatus_ (Bosc.) Curtis.
    b. _Ctenocephalus_ _felis_.
    c. _Ctenophthalmus_ _bidentatiformis_ (Wagner) Baker.
    d. _Ctenopsyllus_ _musculi_ (Duges) Wagner.
    e. _Pulex_ _brasiliensis_ Baker.
    f. _Pulex_ _irritans_ Linnaeus.
    g. _Xenopsylla_ _cheopis_ Rothschild.
4. _Mus_ _rattus_, the black rat.
    a. _Ceratophyllus_ _fasciatus_ (Bosc.) Curtis.
    b. _Ceratophyllus_ _anisus_ Rothschild.
    c. _Ctenocephalus_ _felis_.
    d. _Ctenophthalmus_ _agyrtes_ (Heller).
    e. _Ctenopsyllus_ _mexicanus_ Baker.

f. _Ctenopsyllus_ _musculi_ (Duges) Wagner.

g. _Echidnophaga_ _gallinaceus_.

h. _Pulex_ _brasiliensis_ Baker.

i. _Pulex_ _irritans_ Linnaeus.

Family Sciuridae

1. _Arctomyinae_, ground squirrels.

    a. _Ceratophyllus_ _acamantis_ Rothschild.

    b. _Ceratophyllus_ _bruneri_ (Baker) Wagner.

    c. _Ceratophyllus_ _proximus_ Baker.

    d. _Ceratophyllus_ _silantiewil_ Wagner.

    e. _Ceratophyllus_ _wickhami_ (Baker) Wagner.

2. _Sciurinae_, tree squirrels.

    a. _Ceratophyllus_ _alaskensis_ Baker.

    b. _Ceratophyllus_ _bruneri_ (Baker) Wagner.

    c. _Ceratophyllus_ _proximus_ Baker.

    d. _Ceratophyllus_ _tesquorum_ Wagner.

    e. _Ctenophthalmus_ _orientalis_ (Wagner) Baker.

    f. _Ctenophthalmus_ _setosa_ (Wagner) Baker.

    g. _Pulex_ _anomalus_ Baker.

    h. _Pulex_ _dugesii_ Baker.

Primates

1. _Homo_ _sapiens_, man.

    a. _Ctenocephalus_ _canis_ (Curtis) Baker.

    b. _Pulex_ _irritans_ Linnaeus.

    c. _Sarcopsylla_ _penetrans_ (Linnaeus) Westwood.

# CHAPTER X

## THE BITING AND FEEDING OF FLEAS

### A. HOW THE PUNCTURE IS MADE

A puncture is made in the skin by the epipharynx. The mandibles are inserted in this opening and by their serrations and independent movement, enlarge the opening so that they and the epipharynx penetrate deeper and deeper allowing the points of the maxillae to rest upon the cutaneous surface. The labium doubles back, the V-shaped groove of this organ grinding the mandibles on either side. The labial palpi serve as a protective case when the organs are not in action.

The action of the proboscis is executed with a forward movement of the head and a lateral and downward thrust of the entire body. As the mouthparts are inserted, the abdomen rises simultaneously. The hind and middle legs are elevated while the forelegs are doubled under the thorax, the tibia and tarsi resting firmly on the epidermis serve aa a support for the body during feeding. The maxillarly palpi are retracted beneath the head and thorax. The labium continues to bend, at first as a sheath for the sawing mandibles, and as these are more deeply inserted, it bends beneath the head with the elasticity of a bow forcing the mandibles into the wound until the maxillae are embedded in the skin of the victim. When the proboscis is fully inserted, the abdomen ceases for a time its lateral swinging.

The acute pain of biting is first felt when the mandibles have not quite penetrated and subsequently during each distinct movement of the abdomen.

During the process of penetration the salivary pump receives saliva from the salivary glands and pumps it down, through the channel into the mandibles, into the wound. When the mandibles are retracted the salivary pump collapses, thereby forcing the saliva out with the movement upward of the mandibles.

The swinging of the abdomen gradually ceases as it becomes filled with blood. The stinging of the biting gradually becomes duller and less sensitive as feeding progresses. The movement of the abdomen grows feebler as the downward thrusts of the labium become less frequent.

As the feeding process advances one can discern through the translucent walls of the abdomen a constant flow of blood, caudally from the pharynx, accompanied by a peristaltic movement. When full, the muscles operating the aspiratory pharynx relax from before backward and the pharynx, by means of the elastic reaction of its chitinous lining, contracts and forces the blood backward through the gizzard and into the stomach. The finger-like processes in the gizzard probably act as valves to prevent regurgitation from the stomach.

The end of the meal is signified in an abrupt manner. The flea shakes its entire body, and gradually withdraws its

proboscis by lowering the abdomen and legs and violently twisting the head. When starved for several days the feeding process is much more vigorous. When disturbed the flea shakes its head even while the rostrum is inserted, the mouth-parts are withdrawn and the flea hops away.

## B. THE READINESS WITH WHICH DIFFERENT FLEAS BITE MAN

McCoy (1910c) reports that Ceratophyllus acutus Baker is capable of carrying plague among ground squirrels and that this species readily attacks man under experimental and natural conditions.

Chick, Harriette, and Martin (1911) starved fleas for periods varying from 24 hours to 14 days before testing their inclination to bite man. The test tubes containing the fleas were then inverted upon the naked skin of the subject and the flea carefully watched for a period of two minutes. If the flea did not bite during this period it was regarded as negative for this experiment. Frequently the fleas attached themselves to the subject instantly or within a few seconds and began to feed without delay; sometimes they took a little longer to get started, but usually if they were going to bite at all they did so before one minute had elapsed. The proportion of fleas which bit varied from 36% to 77%, giving a mean for man of 59.6%. Ceratophyllus fasciatus readily bites man. Out of 517 experiments 308 fed, or 59% were positive. In 101 experiments, under identical

circumstances with a rat, 59, or 58.4% of the fleas fed. The experiments performed with C. fasciatus were made upon eight persons and evidence was obtained of preference on the part of the flea for particular indiviuals.

Strickland (1914) confirms the observations of Chick, Harriette, and Martin. He found that C. fasciatus will readily feed on man, but that fleas which have fed only on human blood could never be induced to lay eggs. C. fasciatus was also observed to feed on rabbits and mice.

C. fasciatus, when hungry, readily bites man. There is no reason to suppose that, other things being equal, C. fasciatus would not be as efficient an agent in the transmission of plague from rat to man as Xenopsylla cheopis has been shown to be in India.

Out of 11 experiments made with 46 specimens of Ceratophyllus musculi, Chick, Harriette, and Martin (Op. cit.) found that only 4 fed on man, where-as 9 out of 11 fed on a mouse.

Chick, Harriette, and Martin (loc. cit.) tried 68 specimens of Ctenophthalmus argyrtes, in some cases upon three persons. None of these fed, where-as 11 out of 19 of the same fleas fed on a rat under identical conditions.

Galli-Valerio (1902) placed a variety of Pulex avium taken from a Chelidon urbica upon his body and the body of a colleague. Although this flea had been fasting for some-time it is said not to have made a wound upon either Galli-

Valerio or his colleague.

In regard to _Pulex cheopis_ the Advisory Committee (1907) has shown in the laboratory that this flea readily attacks man. It is said that _P. cheopis_ when very numerous will bite man even in the presence of its natural host. Fleas were often taken from the legs of a number of men who had entered a godown infested with _P. cheopis_ and from those who had entered the rooms of a building in Bombay which was infested with rat fleas. From these observations it is concluded by the Advisory Committee that the rat flea, _Pulex cheopis_, under certain circumstances, is attracted by man, and will readily bite and feed on him.

Galli-Valerio (1902) reports that he was bitten by numerous members of _Pulex erinacei_. Of those which were allowed to run free on his body he felt no bites, but those under the glass bell bit him slightly. These experiments were made only on Galli-Valerio himself. They are regarded, however, as being somewhat significant for he had previously been bitten by _Pulex irritans_ and _Pulex serraticeps_.

Galli-Valerio (loc. cit.) was not bitten by _Pulex fasciatus_ even though the fleas were fasting. Tidswell (1903) states that he was bitten on one occasion by _P. fasciatus_. _Pulex goniocephalus_ when taken from a rabbit and placed on the body of Galli-Valerio did not bite. _Pulex irritans_, the human flea, has been found, sometimes in considerable numbers on rats (_Mus norvegicus_) by Wherry

(1908). Wherry states that he has absolute evidence that squirrel fleas occur on rats and that squirrel fleas occur on, and are known to bite human beings.

Tidswell (1903) states that Pulex serraticeps is known to bite man. In regard to this species Galli-Valerio (Op. cit.) states that he has examined numerous rats without ever finding a specimen and that they are scarce on rabbits. Galli-Valerio and Tidswell report that Typhlopsylla musculi does not bite man. Chick, Harriette, and Martin (1911) state that Xenopsylla cheopis, when hungry, readily bites man.

# CHAPTER XI

## CAPACITY OF THE FLEA'S STOMACH AND THE EFFECTS OF PASSAGE OF *B. PESTIS* THROUGH THE ALIMENTARY TRACT OF THE FLEA

### A. CAPACITY OF THE FLEA'S STOMACH

The average capacity of a rat flea's stomach has been estimated as 0.5 cubic mm. by the Advisory Committee (1907). Thus a rat flea imbibing blood from a plague infected rat might receive as many as 5000 germs in its stomach. Fleas fed on plague-infected rats until the death of these animals, were found on dissection to contain a number of plague bacilli. These bacilli were found to be present up until the 12th day. Multiplication of the plague bacilli must take place in the flea's stomach. The percentage of fleas which had been taken from septicemic plague rats, found with abundant plague bacilli in their stomach contents, varied with the season, this percentage was greatest for the first four days, but a certain number were found infected up to the twelfth day. On one occasion the stomach contents of a twenty day flea were found full of plague bacilli. In the non-epidemic season no flea was found with plague bacilli in its stomach after the 7th day. The rectal contents and feces of fleas taken from septicemic plague rats often contain abundant virulent plague bacilli. One series of experiments made during the epidemic plague season to test the duration of infectivity of rat fleas

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on septicemic rat's blood showed that these fleas could remain infective for at least ten days. A second series of experiments gave the time that the fleas may remain infective as 15 days. In a third series of experiments conducted under the same conditions as the preceding ones, but during the non-epidemic season give the time as 7 days in which the fleas might remain infective.

### B. POSSIBILITY OF THE CONVEYANCE OF B. PESTIS BY FLEAS WHICH HAVE FED ON SEPTICEMIC BLOOD

Fleas which have fed on septicemic blood are capable of conveying infection to fresh animals on which they feed. This capability is associated with the presence of the plague bacilli in the stomach, intestines, and feces. If such infected fleas be kept in captivity, it is found that after a time they are no longer capable of conveying infection; at the same time on dissection no bacilli are found in them. These conditions led to the idea of the existence of a clearing process.

### C. THE EXISTENCE OF A CLEARING PROCESS

It is said by the Advisory Committee (loc. cit.) that the existence of a clearing process was suggested by the fact that after feeding on the same septicemic blood the number of bacilli in the stomach of a batch of fleas varied. A few hours after feeding all degrees of infection, varying

from crowded masses to such small infections that it was only by a continued search that any bacilli were recognized, In about 50% of the fleas, the Advisory Committee found no bacilli by microscopical examination. It is further reported by the Advisory Committee that if a number of fleas be fed upon a septicemic rat and subsequently kept under observation, being meanwhile nourished upon healthy animals, the proportion found to be infected steadily diminishes day by day. At the same time a considerable mortality occurs so that the decrease in the infected fleas might be due to those harboring plague bacilli dying more rapidly than those not infected.

To ascertain whether such was the case the Advisory Committee performed several experiments with infected and healthy fleas and the mortality compared. The results show that no greater mortality occurs among healthy fleas under the same conditions. From these experiments it seems that the presence of the plague bacillus in the stomach and gut of the flea does not materially affect the health of the insect.

The bacilli multiply in the blood of the rat which is taken into the stomach but they are at the same time subjected to all the influences which blood is capable of exerting on bacteria. These influences will be most active immediately after a meal and gradually lessen as the blood becomes altered by the digestive process. Phagocytosis is placed by the Advisory Committee (1907) as the most

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important of these influences.

If a well infected flea be fed on fresh blood and after the lapse of some fifteen minutes be killed and a film of the stomach contents stained with Leishman's stains, the poly-nuclear cells are seen to be engorged with plague bacilli. Experiments showed that a rise of temperature of about 8 degrees C. doubles the rate at which the bacilli disappear.

The presence of plague bacilli in the stomach of the flea, and the length of time that they persist therein, is largely influenced according as the bacilli are subjected to the action of fresh blood immediately after the infecting meal or not; so that the extent of infection is dependent on whether it feeds on healthy blood immediately after its infecting meal, or whether it is starved for a while. Experiments show that twice as many starved fleas had bacilli in their feces as fed fleas on the same day.

It appears, therefore, that a flea starved after the ingestion of septicemic blood offers the greatest chances of conveying infection, and that these chances are diminished if the insect has in the meantime taken a meal of normal blood, and that the meal of the blood of an immunized animal still further diminishes the infectivity of these insects. A probable explanation is offered by the discovery that the plague bacilli remaining in the stomach are readily ingested by the leucocytes taken in with the second meal and such

phagocytosis might be expected to be more pronounced in the case of immune blood.

## D. TIME FLEAS CARRYING B. PESTIS ARE ABLE TO SURVIVE AND REMAIN INFECTIVE

Bacot (1915) lists the following conclusions from a series of experiments to determine the length of time that fleas (Ceratophyllus fasciatus) carrying Bacillus pestis in their alimentary canals are able to survive in the absence of a host and retain the power to re-infect with plague. (1) Fleas (C. fasciatus) are able to carry B. pestis for periods up to 47 days in the absence of any host and subsequently to infect a mouse. (2) That infected fleas, starved for 47 days and then placed upon a mouse, may not infect it for a further period of about 20 days. Bacot further states that there is no reason to suppose that the positive results obtained in these few experiments represent the limit of time after which infection may take place, but indicate that plague infection may persist in fleas for one or two months in cool weather and subsequently, give rise to an epizootic.

## E. THE INFECTIVITY OF THE GUT OF FLEA LARVAE

Bacot (1914) undertook several experiments to decide (a) if the gut of flea larvae may become infected with bacteria that are present in the food on which they are nourished; for example, the feces of their parents, and (b)

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if these organisms can survive within the gut during the metamorphosis from larva to pupa and from pupa to imago. The number of cases in which microscopic examination gave a positive result was very small and the bacilli, when present, were few and scattered. No trace was found of the mass multiplication which is so noticeable a feature in infected adult fleas.

# CHAPTER XII

## THE EXPERIMENTAL TRANSMISSION OF PLAGUE

### A. TRANSMISSION OF PLAGUE FROM GUINEA PIG TO GUINEA PIG

McCoy (1909b) took a flea (_Ceratophyllus acutus_) from a squirrel (_Citellus beecheyi_) which died of acute plague. The flea was crushed between two microscopical slides. The film on one of the slides was fixed and stained, and an enormous number of organisms were found which were indistinguishable in size and shape from _B. pestis_. The remains of the crushed flea were removed from the second slide with a small pledget of absorbent cotton moistened with physiological solution of sodium chloride. The cotton carrying fragments of the flea was placed in a small packet under the skin of the belly of a guinea pig. The guinea pig died 8 days later and showed characteristic lesions of plague. _B. pestis_ was recovered in pure cultures from the liver of the guinea pig.

McCoy (1910b) after freeing a California ground squirrel (_Citellus beecheyi_) of fleas, inoculated this squirrel with a culture of _B. pestis_ that had been carried for a long time on artificial media. On the 5th day after inoculation, 89 squirrel fleas (_Ceratophyllus acutus_ Baker) were put in the cage with the animal. The squirrel died 4 days later. A few hours after the death of the squirrel 4 guinea pigs were placed in the cage, the body of the squirrel being permitted

to remain with them for about half an hour. The body of the squirrel was then removed and subjected to a post-mortem examination and the lesions of sub-acute plague were found. One of the guinea pigs died on the 8th day and another on the 12th day. Each animal exhibited the lesions of sub-acute plague. The remaining guinea pigs were chloroformed on the 16th day and found entirely healthy.

In this experiment the possibility of contagion from the contamination of the cage and from the body of the squirrel could not be eliminated; however, the mass of evidence against such modes of infection is so great as to leave practically no doubt that the transmission was by means of the fleas introduced.

In another experiment McCoy (1910b) inoculated a ground squirrel with a culture of the plague bacillus derived from a case of plague in man (squirrel origin). 48 hours after inoculation 100 fleas (Ceratophyllus acutus) were placed in the cage with the squirrel. This squirrel died upon the 5th day, and at the autopsy showed the usual lesions of acute plague. 27 fleas were recovered from the body of the rodent. 2 of the fleas were crushed and each showed in smears an abundance of pest-like bacilli. The remaining 25 fleas were placed in a clean cage with a healthy squirrel. This 2nd squirrel died on the 10th day, presenting at autopsy the characteristic lesions of sub-acute plague. A culture of B. pestis was isolated from the liver. This experiment

proves conclusively that squirrel fleas may carry plague infection from one squirrel to another, but whether this is the usual mode of conveyance in nature remains to be proven. The fleas used in these experiments were bred on healthy squirrels in the laboratory and had never had an opportunity to become contaminated prior to the experiment.

The Advisory Committee (1906) performed a number of experiments in the plague houses of Bombay to determine the relation of fleas to the spread of plague. Guinea pigs allowed to run free in plague houses acted as good traps for fleas. In 29 per cent. of these plague rooms the guinea pigs left in from 18-40 hours contracted plague. Plague houses which had been disinfected by the ordinary means, still contained fleas in large numbers, an average of 40 fleas per house having been taken in 31 observations. Further, 29 per cent. of these disinfected houses were infective for guinea pigs allowed to run free in them. On three occasions--namely, every occasion on which the experiments were made, fleas transferred from plague-infected rats in houses in Bombay were able to transmit the disease to healthy animals in flea-proof cages in the laboratory.

Forty-two experiments were made, in which two animals, one protected from fleas by means of a wire gauze curtain, the other not so protected, were placed side by side in a plague house. Both animals were protected from soil infection

and from infection by contact with animals outside, but were equally subject to aerial infections. While not one of the protected animals contracted plague, four of the unprotected ones died of this disease. The number of fleas caught on the unprotected animals was very many times less than the number taken on the guinea pig running free in the experiments of the first group. No fleas were caught on the protected animals.

Animals protected from fleas by means of a sufficiently broad layer of "tangle-foot" and placed in plague infected houses do not contract plague, but the control animals, not so protected, on several occasions (24 per cent.) developed the disease. Out of 247 fleas caught on the "tangle-foot" 60 per cent. were human, 34 per cent. were rat and 6 per cent. were cat fleas. Plague-like bacilli were demonstrated in the stomach contents of one of 85 human fleas dissected, and of 23 out of 77 rat fleas.

The work of the Advisory Committee (1907) substantiates and confirms the work done by this commission in 1906. It may be added that they stated that fleas and fleas alone, were the transmitting agents of infection in their experiments.

B. TRANSFERENCE OF PLAGUE FROM RAT TO RAT

The Advisory Committee ( 1906) repeated the experiments of Gauthier and Raybaud (1902, 1903) and showed that in the presence of the common Indian rat flea (<u>Pulex</u> <u>cheopis</u>

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Rothschild) plague may be spread from a plague-infected rat to a healthy rat confined in close proximity, but in such a way as to prevent contact with the body or excreta of the sick rat. Thus on 30 occasions healthy rats contracted plague by living in the neighborhood of a plague-infected rat under circumstances which prevented the healthy rat coming in contact with the body or excreta of the plague-infected rat. In all cases a fairly abundant supply of fleas were present. These fleas could pass freely between the two rats, and, except for "aerial contagia", formed the only apparent means of communication between the animals. The presumption is that plague was transferred from the sick to healthy rats by the agency of fleas.

In another series of experiments the Advisory Committee transferred fleas collected from infected rats to healthy English white rats. In 8 out of 13 completed experiments, the rats which received the fleas died of plague, while in five instances they remained healthy.

In 21 out of 38 experiments in which fleas were transferred from Bombay rats dead of septicemic plague to healthy Bombay rats, healthy rats living in flea-proof cages contracted plague in sequence to receiving fleas collected from rats dead or dying of septicemic plague in another cage.

The Advisory Committee (1906) states that epidemic infection spreads readily enough from rats inoculated with plague to healthy rats living with them if a large number

of rat fleas are present, and that under precisely the same conditions, except that the fleas are absent or present in very small numbers, no epidemic occurs. In no case did an epidemic arise in the absence of fleas, though in three cases there was no material spread of infection though fleas were plentiful.

## C. TRANSMISSION OF PLAGUE FROM RAT TO MAN

Clemow (1900) states that in rare instances it has seemed possible to state definitely that an infected rat has given the disease directly and immediately to a human being, either under circumstances which leave no doubt as to the manner in which the infection was transmitted ( as by a bite) or in some manner less obvious (as by merely touching the animal). It is further stated that in the large majority of instances the mode in which the infection passes from rat to man is quite uncertain, and that there is often much room to doubt whether any such transmission has in fact taken place, or whether men and rats have not both caught the infection from some common source to which they have been exposed. The direct transmission of plague from rat to man by means of a bite from an infected animal is said to be quite rare. Of much more common occurrence, however, is the development of plague in persons who have handled a living or dead rat infected by the disease. Clemow concludes that rats can, and do suffer

from plague under natural conditions; that they can and do act as a means of diffusing infection and transmitting it to man; but that the extent to which they are responsible for the diffusion of the disease and the distance over which they diffuse it is uncertain.

Browning-Smith (1906) uses the time interval between importation and rat mortality and between rat mortality and the real epidemic as a basis for believing that the rat is the necessary link in the chain of infection. He estimates the first time interval as being from 3 to 7 days and the second one as being from 3 to 10 days. The interval between the imported case and the first case of the epidemic should be much shorter according to Browning-Smith if the infection passes direct from man to man.

The Advisory Committee (1907) from epidemiological observations made by the commission in Bombay city summarize their conclusions regarding the inter-relations of the epidemic and the epizootic as follows: (1) The time relation of the epidemic and the rattus epizootic is explicable on the view that the rat flea is the transmitting agent of the infection from <u>Mus rattus</u> to man. (2) From the point of view of plague infection there is an intimate relation between the epidemic and the rattus epizootic. (3) There is a definite quantitative relation between the incidence of human and rat plague. (4) The epidemic is directly attributable to the rattus epizootic and since this epizootic

is in its turn directly attributable to the latter epizootic.
(5) Infection is occasionally transferred directly from *Mus decumanus* to man, without the intervention of *Mus rattus*.

# CHAPTER XIII

## CONCLUSION

*Bacillus pestis* was discovered and studied by Kitasato and Yersin, working independently at the same time (1894) during the epidemic of plague at Hongkong. *B. pestis* is always found in the affected glands of well-marked cases of plague, in the buboes, in the blood and tissues of the septicemic variety, and in the lungs and sputum of pneumonic types of plague. *B. pestis* is non-motile and readily stains by aqueous solutions of methylene blue, gentian violet, fuchsin, or any ordinary basic dyes, but it is not stained by Gram's method unless a weakened solution of 50% is used instead of absolute alcohol for the decoloration process. The characteristic growth of *B. pestis* on bouillon and the presence of involution forms are two important features by which the bacillus might be recognized. Moisture and temperature are important factors in the growth of the bacillus.

There are several symptoms which are characteristic for all types of plague of the severe type. These symptoms are the peculiar expression of the face, the halting speech, and the condition of the tongue. The different forms of plague are: (1) the bubonic type, (2) the pneumonic type, (3) the septicemic type, (4) mild plague, (5) cutaneous plague, (6)

tonsillar plague, (7) sylvatic, (8) intestinal, (9) cerebral, (10) puerperal, and (11) the typhus type.

It is generally concluded by a number of investigators that birds; namely, pigeons, ducks, turkeys, and chickens are not susceptible to plague. Bandicoots, gophers, rats, and squirrels are susceptible to plague under natural conditions. Plague may be produced in rabbits, mice, and monkeys artificially in the laboratory.

The Siphonaptera are divided into eight families; namely, Rhynchoprionidae, Hectopsyllidae, Malacopsyllidae, Lycopsyllidae, Pulicidae, Ctenopsyllidae, Hystrichopsyllidae, and Ceratopsyllidae.

The body of the Siphonaptera is laterally compressed thus making it easy for the insect to work its way through the hair or feathers of its host. The body is divided into a head, thorax, and abdomen. The head is attached directly to the thorax without the intervention of a neck. The internal anatomy of the flea is characteristic of that of insects in general.

The life history of fleas includes four distinct stages: egg, larva, pupa, and adult. The breeding places of the different species vary with the habits of the host. The eggs are deposited by the female flea in places where the host usually sleeps. Climatic conditions, temperature, and lack of food have definite effects upon the number of eggs deposited. The length of life and the rapidity with which

the flea develops depends upon the nature of the surroundings of the flea.

The length of life without food depends upon the environment of the flea. The average length of life is considerably longer in low temperatures (12.77 to 18.33 degrees C.) than in room temperature (12.77 to 29.44 degrees C.).

The average capacity of the rat flea's stomach has been estimated as 0.5 cubic mm. A rat flea thus imbibing blood from a plague infected rat may receive as many as 5000 germs in its stomach. Fleas which have fed on septicemic blood are capable of conveying the infection to fresh animals on which they feed. It appears that a flea starved after the ingestion of septicemic blood offers the greatest chances of conveying infection, and that these chances are diminished if the insect has in the meantime taken a meal of normal blood, and that the meal of the blood of an immunized animal still further diminishes the infectivity of these insects. Fleas (Ceratophyllus fasciatus) are able to carry Bacillus pestis for periods up to 47 days in the absence of any host and subsequently to infect a mouse.

The Advisory Committee (1906) has shown that in the presence of the common Indian rat flea (Pulex cheopis Rothschild) plague may be spread from a plague-infected rat to a healthy rat confined in close proximity, but in such a way as to prevent contact with the body or excreta of the sick rat. Thus on 30 occasions healthy rats contracted

plague by living in the neighborhood of a plague-infected rat under circumstances which prevented the healthy rat coming in contact with the body or excreta of the plague-infected rat. In all cases a fairly abundant supply of fleas were present. These fleas could pass freely between the two rats, and, except for "aerial contagia", formed the only means of communication between the animals. The plague was transmitted from the sick to healthy rats by fleas.

Fleas play a very important part in the transmission of Bacillus pestis from rat to rat, squirrel to squirrel, and from rat to man.

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